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BIRDS OF NORTHERN BLACK MESA, NAVAJO COUNTY, ARIZONA

Charles T. LaRue[1]

*You should see the glorious color when
the first light of dawn spreads on the
golden cliff tops and the blue-grey
pinyon clad slopes.*

Everett Ruess
Chilchinbito, Arizona
May 5, 1934

Abstract.—Two hundred forty-one species of birds have been identified from northern Black Mesa, Arizona. This region's avifauna was poorly known until the late 1970s when large-scale coal mining began. Vegetation of the region is predominantly Great Basin desert scrub, pinyon-juniper woodland, and mixed-conifer woodland. The latter vegetation type supports an assemblage of isolated montane bird species unique to the region. Numerous environmental changes have recently affected the bird life of Black Mesa. These include large-scale type conversions (pinyon-juniper clearing and surface mining), pond construction, and establishment of exotic vegetation.

Key words: Arizona, Black Mesa, Navajo reservation, Hopi reservation, avifauna survey, bird-habitat relationships, bird density, species listing, breeding birds, coal mining.

Black Mesa covers a remote expanse of 850,000 ha (2.1 million ac) of uplands on the Navajo and Hopi Indian reservations in northeastern Arizona (Fig. 1). The physical isolation of this region has made detailed and extensive biological surveys difficult to conduct; in some areas no such surveys have been done. Information on bird life is particularly scant. Phillips et. al (1964) refer to a "severe lack of data" for the birds of northeastern Arizona. Maps of the most recent annotated checklist of Arizona birds (Monson and Phillips 1981) show a large blank spot centered on Black Mesa.

The casual traveler driving Highway 160 through Kayenta or visiting Monument Valley might notice the paucity of life in the area but would be unaware of the diverse environment behind the nearby scarp of Black Mesa. Hidden in the rugged complex of canyons and valleys along the highest northern portions of Black Mesa is a diverse assemblage of vegetative

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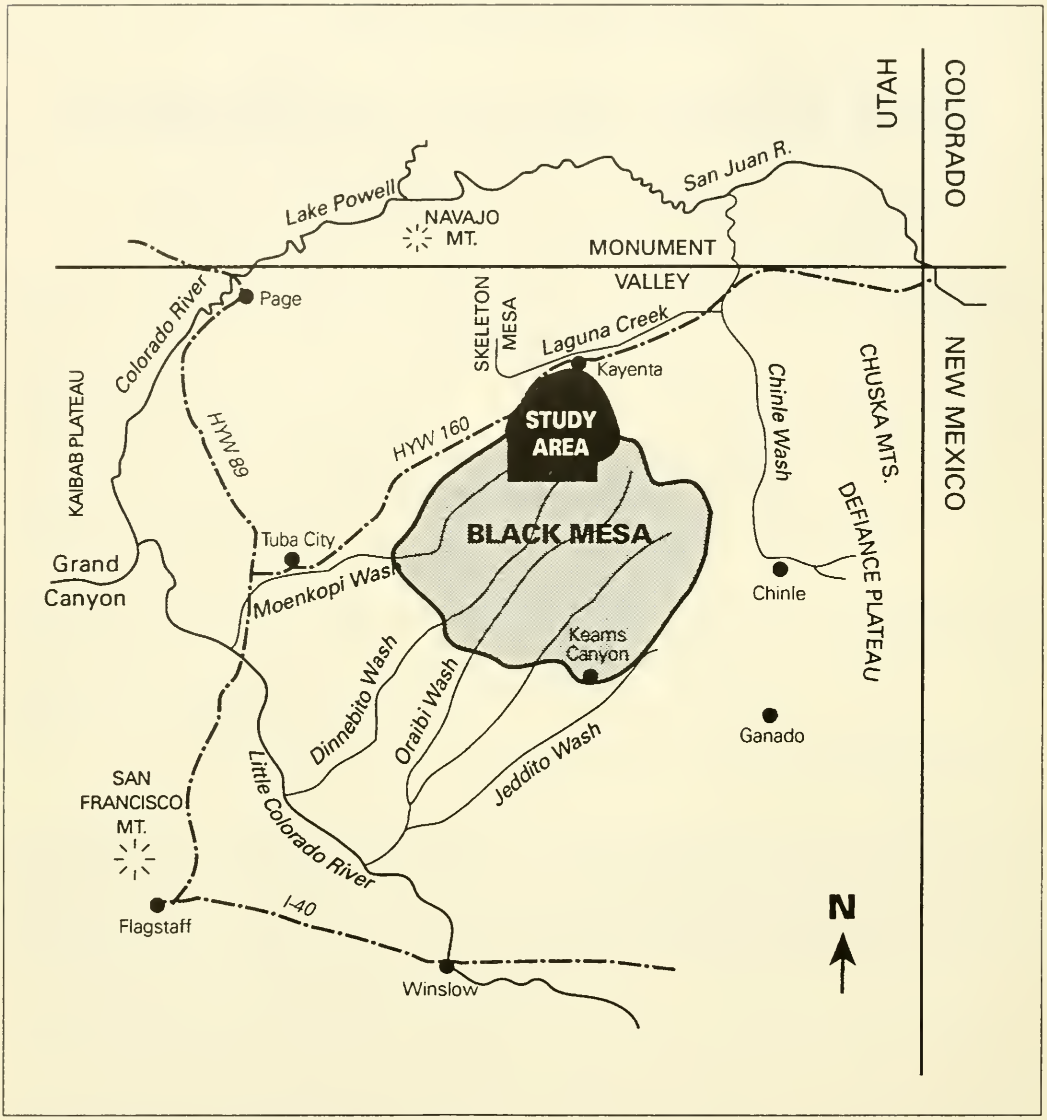
UTAH
COLORADO
NEW MEXICO
Lake Powell
NAVAJO MT.
San Juan R.
MONUMENT VALLEY
Page
Colorado River
SKELETON MESA
Laguna Creek
Kayenta
KAIBAB PLATEAU
HYW 89
HYW 160
STUDY AREA
BLACK MESA
Chinle Wash
CHUSKA MTS.
DEFIANCE PLATEAU
Tuba City
Grand Canyon
Moenkopi Wash
Chinle
Keams Canyon
Dinnebito Wash
Oraibi Wash
Ganado
Jeddito Wash
SAN FRANCISCO MT.
Little Colorado River
Flagstaff
I-40
N
Winslow

Fig. 1. Northern Arizona and the Black Mesa region.

communities. These communities, some of which are typical of the higher mountains of the Colorado Plateau, support a surprising number of bird species. In a single 260-ha (640-ac) block near Lolomai Point, 45 species are known to breed. If one searched further in this same block or doubled its size, an additional 21 species could probably be found breeding. A total of 241 bird species (including those in the archaeological record) are known from northern Black Mesa. Another 40 species (all migrants) would be included in this list if the boundary of the study area covered in this report were to be moved just a few kilometers north to Laguna Creek at Kayenta (Jacobs 1986, personal records).

The purpose of this report is to present what is currently known of the birds of northern Black Mesa and to discuss some ecological factors affecting them. This includes reporting the status of all bird species recorded on northern Black Mesa in the late 1970s and the 1980s, reporting the avian assemblages associated with each habitat found in this area, discussing possible causes and effects of environmental changes that impact bird communities of the area, and providing a sound base for future work on the bird life of the mesa.

METHODS

A review of historical accounts and other publications was conducted to determine the extent of previous explorations and studies on northern Black Mesa. Results of this search and discussions with Gale Monson revealed the poor state of knowledge of the area's avifauna prior to the 1970s.

Variable width transects (Emlen 1971, 1977) were used to derive bird densities in different habitats on the Peabody Coal Company leasehold as part of the federally required baseline wildlife surveys. Each transect was usually about 1500 m long and was traversed three times each season.

Spot-mapping grids were established in three pinyon-juniper stands to census breeding bird densities in 1983 and 1984. Spot-map censuses were also conducted in mixed-shrub habitat from 1984 to 1986 and in three reclaimed mine spoil sites in 1985. These results are reported as number of pairs/40 ha. When presenting population density data from the literature, I have converted all values to number of individuals or number of pairs per 40 ha if this was not done by the authors.

Waterfowl and shorebirds were counted at ponds during migratory periods in 1982 and 1983. Each spring from 1982 until present, a survey for nesting raptors within the Peabody lease was conducted. Nest sites located in any previous year were checked for use, and searches for new nesting sites were conducted.

The area north of the Peabody Coal Company lease and the area below the rim of the mesa are unaffected by the Surface Mining Control and Reclamation Act (SMCRA) and, therefore, were not baseline surveyed. I visited these areas on over 250 occasions from December 1981 through 1993, covering over 1770 km (1100 miles) by foot. On these visits I tried to determine the presence and status of those bird species that utilize this area. Many observations from throughout the area are incidental.

The faunal resemblance index (see Table 12) used to compare the breeding bird composition of each habitat is that applied by Hoffmeister (1986) to Arizona's mammalian fauna. Because of the variety of techniques used to determine bird densities in the lease area and the lack of density data for habitats outside the lease area, the usual techniques employed to determine similarity values for bird data were not used. These resemblance factors are based on the number of species shared in common between habitats and provide adequate comparisons of the degree of similarity between the breeding bird composition of the habitats across the entire study area.

Classification, sequence, and common and Latin names follow the American Ornithologists Union (1983, 1985, 1987, 1989). Latin names of birds are presented only in the species accounts. Common and Latin names of plants, in general, follow McDougall (1973). Common names of birds are capitalized following the opinion of Potter (1984). Geographic place names and spellings are from U.S. Geological Survey 7.5-minute topographic quadrangles. Additional names are my own creation, e.g., "east," "middle," and "west" forks of Coal Mine Wash (Fig. 2). The "upper," "middle," and "lower" portions of washes refer to the upper third, middle third, and lower third, respectively, of those portions of each wash *within the study area.* Other names are those used by Peabody Coal Company. Figure 2 presents locality names used in this report.

The periods of the month are as follows: early (1st–10th), mid (11th–20th), late (21st–end). Plumage terminology follows that of Humphrey and Parkes (1959). Terms of subjective abundance follow Monson and Phillips (1981): abundant—in large numbers; common—always to be seen, but not in large numbers; fairly common—very small numbers or not always seen; uncommon—seldom seen, but not a surprise; sparse—always a surprise, but not out of normal range; casual—out of usual range, to be expected every 20–50 years; and accidental—far from normal range and not to be expected again. The term *area* refers to the study area of this report. The term *region* refers to all of Black Mesa, Kayenta Valley, eastern Shonto Plateau, and Tsegi canyons. *Lease* means the Peabody Coal Company leasehold. Proof or confirmation of breeding consists of the following: nests with young and/or eggs, fledglings with or without adults, and remains of fledglings. Breeding is

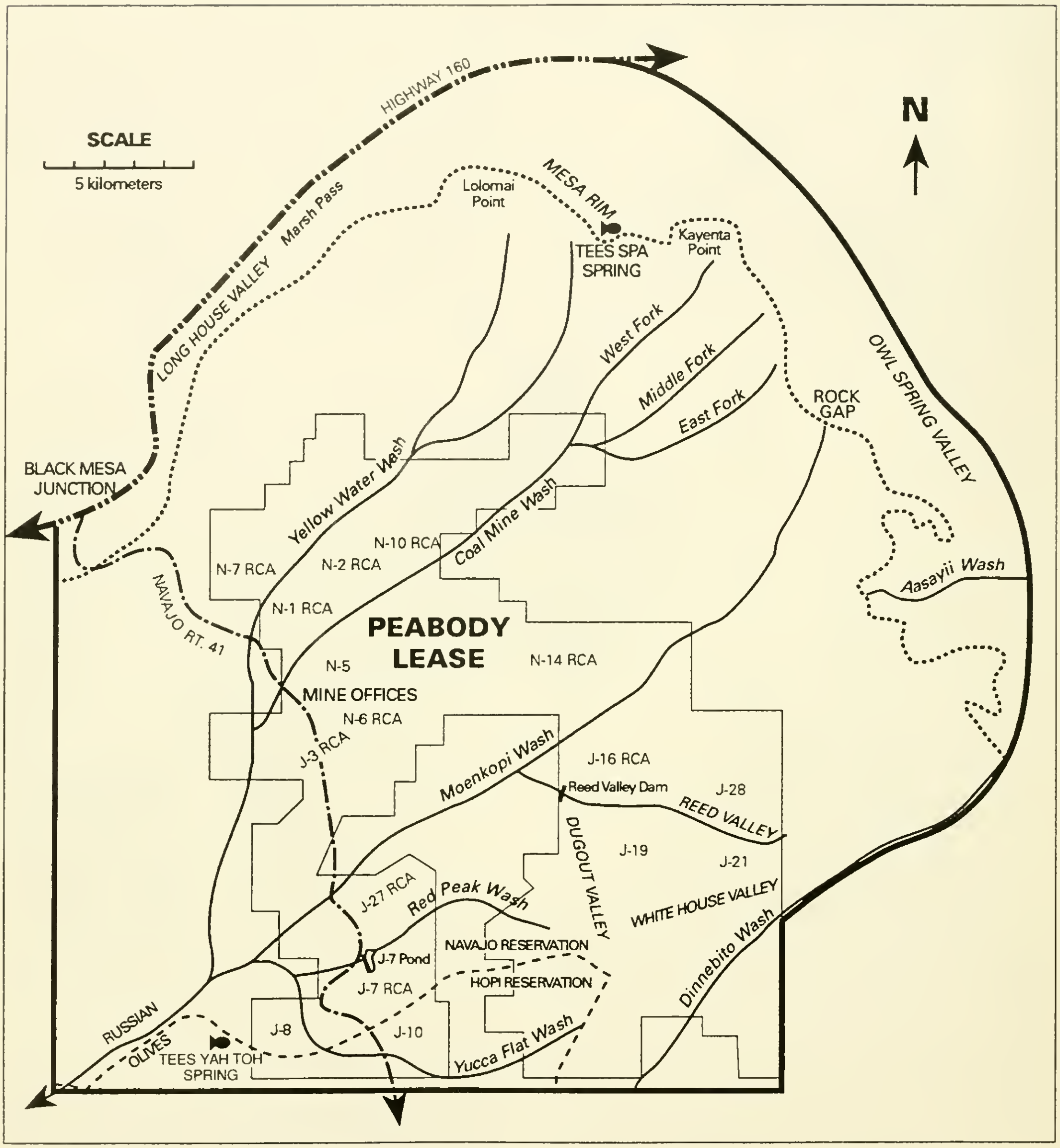
HIGHWAY 160
N
SCALE
5 kilometers
Lolomai Point
MESA RIM
TEES SPA SPRING
Kayenta Point
Marsh Pass
LONG HOUSE VALLEY
West Fork
Middle Fork
East Fork
ROCK GAP
OWL SPRING VALLEY
BLACK MESA JUNCTION
Yellow Water Wash
Coal Mine Wash
N-10 RCA
N-7 RCA
N-2 RCA
N-1 RCA
Aasayii Wash
NAVAJO RT. 41
PEABODY LEASE
N-5
N-14 RCA
MINE OFFICES
N-6 RCA
J-3 RCA
Moenkopi Wash
J-16 RCA
Reed Valley Dam
J-28
REED VALLEY
DUGOUT VALLEY
J-19
J-21
J-27 RCA
Red Peak Wash
WHITE HOUSE VALLEY
NAVAJO RESERVATION
J-7 Pond
HOPI RESERVATION
J-7 RCA
Dinnebito Wash
RUSSIAN OLIVES
J-8
J-10
Yucca Flat Wash
TEES YAH TOH SPRING

Fig. 2. Locality names of the study area used in text.

suspected when territorial or singing adults have been found frequently in the proper habitat in two or more breeding seasons.

The seasons are defined as winter—December through February; spring—March through May; summer—June through August; and fall—September through November. Early, mid, and late seasonal references refer to the first, second, and third months of each season, respectively. A *permanent resident* is a species that is present in the study area in all four seasons. A *summer resident* is a species that is present in the study area primarily in summer. Certain summer residents arrive, however, in winter and leave in the fall. Likewise, some summer residents may be more numerous as fall or spring migrants. *Winter residents* are species that spend the winter period and/or portions of fall and spring, but do not remain to breed. *Migrants* are species that pass through the area but do not overwinter or breed. *Transient* is generally synonymous with migrant but refers to species or individuals that wander infrequently through the study area.

Subspecies are dealt with primarily in reference to species known or suspected to breed in the study area. The only specimens collected on Black Mesa (or nearby) consist of few individuals of few species. These were collected in the 1930s during the Rainbow Bridge–Monument Valley Expedition (Woodbury and Russell 1945). To my knowledge, no recent specimens have been collected in the area. Subspecies that breed in the area are determined from Monson and Phillips (1981), Behle et al. (1985), Woodbury and Russell (1945), and Behle (1985). In several species the race(s) present on Black Mesa (or northeastern Arizona) are unknown, questionable, or transitional. Salvage collecting these species in areas to be mined would help resolve these questions.

HISTORY OF BLACK MESA STUDIES

Northern Black Mesa remained biologically unexplored until the 1930s. Spanish, Mexican, and United States penetrations into this area were military operations undertaken with extreme difficulty (McNitt 1962, 1972). Possibly the first white man to see northern Black Mesa was Colonel Don Francisco Salazar, who crossed "the almost impassible wilderness of Black Mesa" in August 1823 (McNitt 1972). Captain John G. Walker probably passed directly through the study area of this report when he crossed the "high broken ground of Black Mesa" in September 1859 (McNitt 1972). Lieutenant H. P. Kingsbury of Troop K, 6th Cavalry, crossed 117 km (73 miles) of "viciously rough wooded terrain" of the "uninhabited wastes of Black Mesa" on 19–20 August 1884 (McNitt 1962). Apparently, no reports dealing with the natural history of Black Mesa were made following these expeditions.

The series of United States government surveys that traversed the Little Colorado River Valley or skirted the southern fringe of Black Mesa in the late 1800s probably never reached northern Black Mesa (Woodbury and Russell 1945). Since no major trading posts were established on northern Black Mesa, scientists who frequently visited such outposts also never reached the area (Woodbury and Russell 1945, McNitt 1962).

The earliest mention of specific birds observed on Black Mesa is that of Theodore Roosevelt (Roosevelt 1913), when he ascended the mesa after leaving John Wetherill's trading post at Kayenta on 17 August 1912. Roosevelt's route undoubtedly took him through Rock Gap at the head of Moenkopi Wash. He wrote:

> Our first day's march took us up this [the northern escarpment of Black Mesa]. We led the saddle horses and drove the pack animals up a very rough Navajo trail which zigzagged to the top through a partial break in the continuous rock wall. . . . On the summit we were once more among pines and we saw again the beautiful wild flowers and birds we had left onBuckskin Mountain [Kaibab Plateau]. . . . I saw a Louisiana Tanager [Western Tanager]; the pinyon jays were everywhere; ravens, true birds of the wilderness, croaked hoarsely. . . . From the cliff crest we traveled south through a wild and picturesque pass. The table land was rugged and mountainous; but it sloped gradually to the south, and the mountains changed to rounded hills.

Extensive coal deposits helped to end the isolation of Black Mesa. Long before modern exploitation, prehistoric peoples utilized this coal for ornaments, firing pottery, and heating. The Hopi made extensive use of coal on the southern edge of Black Mesa (Hack 1942). During at least A.D. 600–1050, the Anasazi used coal on northern Black Mesa (Gummerman 1984). The first automobile road built over the northern rim of Black Mesa was apparently constructed for the development of coal mines on Yellow Water Wash in the early 1900s (Johnston 1932). It was this road that allowed access by biologists to the high country of the mesa to record the only systematic bird observations prior to the 1970s. Most of these records, concerning less than 40 species, were from a series of trips by H. N. Russell and A. M. Woodbury, participants in the Rainbow Bridge–Monument Valley Expedition in June and July 1938 and in August 1935 and 1937 (Woodbury and Russell 1945). Approximately 24 specimens of 11 species were collected on trips made on 11 and 16 July 1938 and 17 August 1939. Brotherson et al. (1981) studied the bird community composition in Betatakin Canyon, an area similar to the rim region of Black Mesa, at nearby Navajo National Monument. Bradfield (1974) reported on the birds of southern Black Mesa in the vicinity of Oraibi. Jacobs (1986) recently compiled an annotated list of birds from the Navajo and Hopi reservations that includes observations from and around Black Mesa.

Peabody Coal Company studies from 1981 to the present and records that form the core of this report were initiated to meet surface mining regulations. Mining activities were underway on Black Mesa by 1971, but it was not until 1977 with the passage of the Federal Surface Mining Control and Reclamation Act (SMCRA) that detailed studies began. SMCRA requires baseline wildlife censusing as part of the federal mine-permitting process. Peabody Coal Company hired Espey, Huston, and Associates to conduct the initial surveys in the western portion of the 25,900-ha (100-sq-mile) lease in 1979–80. The results were presented in 1981. Peabody Coal Company biologists censused the remainder of the lease area in two units in 1981–82 and 1982–83. Results were presented in 1982 and 1983, respectively. Waterfowl, raptor, and small bird censuses have been conducted from 1982 to the present. I have made several hundred trips north of the lease area into the highest and more remote portions of Black Mesa from 1982 through 1993 recording the birds found there. Therefore, virtually all bird censusing from 1982 to 1993 was conducted by me.

BLACK MESA ENVIRONMENT

Physiography and Geology

Black Mesa encompasses a large expanse of uplands on the Navajo and Hopi Indian reservations in northeastern Arizona (Fig. 1). The mesa is roughly circular and 88–113 km (55–70 miles) across and covers nearly 518,000 ha (2000 sq miles). The mesa itself is in the center of a large structural basin (Repenning and Page 1956); as a result, the interior is lower than the rim on the east, north, and west sides. A network of five large, parallel flowing washes drains Black Mesa to the southwest and empties into the Little Colorado River. These washes, previously called the Tusayan Washes, are (east to west) Jeddito, Polacca, Oraibi, Dinnebito, and Moenkopi. Pinyon and Forrest Lake are the only relatively large communities in the interior of Black Mesa. The larger communities of the region are situated in the valleys surrounding the mesa.

Most of Black Mesa consists of low mesas, rolling hills, and shallow valleys. Elevations rise gradually to the rim, which breaks off in a stair-step escarpment 150–610 m (500–2000 ft) high. Where the large washes exit the mesa, elevations may be near 1680 m (5500 ft), and the rim rises to above 2440 m (8000 ft). Most of the mesa is approximately 1830–2070 m (6000–6800 ft) in elevation.

Black Mesa is underlain by a regionally downwarped series of Jurassic, Triassic, and older sedimentary formations. The topographically elevated portion of the mesa itself is composed of a series of sedimentary beds deposited during a period of transgressing and regressing seas in the late Cretaceous (Repenning and Page 1956). The Jurassic Cow Springs and Morrison formations and the Dakota Sandstone are the oldest deposits to outcrop on the mesa flanks at the northern base. The Mancos shale forms broad slopes at the foot of the mesa and underlies the broad valleys where the major washes leave the mesa. Most of the rocks exposed on Black Mesa are of the Toreva and Wepo formations. The former is composed of cliff-forming pale sandstones that cap small mesas and canyons. The Wepo is a complex of sand, silt, and mudstones that contain significant coal deposits. The rolling baked-clinker hills of the Black Mesa interior are Wepo. The highest portion of Black Mesa along the impressive northern scarp is capped by the Yale Point Formation. This pale, crossbedded sandstone is dissected into a series of short, deep canyons. Recent alluvium is deposited in virtually every valley floor throughout Black Mesa. Aeolian deposits are more extensive on southern Black Mesa than in the northern portions (Cooley et al. 1969).

The area covered in this report is the northernmost portion of Black Mesa south of the town of Kayenta (Fig. 1). This area lies between 36°42′30″ and 36°22′30″N latitude and 110°10′ and 110°30′W longitude. Included here is the upper 16–24 km (10–15 miles) of Moenkopi and Dinnebito washes and their tributaries. It includes the mesa rim from near Black Mesa Trading Post northeast to Lolomai Point and southeast to the head of Assayii Wash. It covers the mesa foot from upper Long House Valley to upper Owl Spring Valley and the upper basin of Assayii Wash (Fig. 2). The 25,900-ha (64,000-ac) Peabody Coal Company lease is located in the southern portion of the study area. The study area encompasses approximately 106,200 ha (232,573 ac). A few bird records reported herein come from outside this specific study area.

Elevations range from 1768 m (5800 ft) at the mesa foot to 2490 m (8168 ft) at the highest point on the rim. Where Moenkopi Wash leaves the study area, the elevation is about 1829 m (6000 ft). The southern portion is typified by pinyon-juniper woodland–covered hills and shrub-filled valleys. To the northeast the land rises gradually and becomes incised by canyons up to 152 m (500 ft) deep. From the rim the mesa breaks off in a spectacular escarpment of cliffs and slopes to grasslands 610 m (2000 ft) below.

Climate

The climate of the study site is semiarid and, as is characteristic of the region, typified by daily and seasonal temperature extremes. Temperatures of –34°C (–30°F) and 40°C (104°F) have been recorded on southern Black Mesa (Thornthwaite et al. 1942). Excellent detailed descriptions of the regional climatic patterns directly applicable to Black Mesa are those of Hack (1942), Thornthwaite et al. (1942), Lowe (1964), and Sellers and Hill (1974). The mean annual temperature of surrounding sites ranges from 11.6°C (53°F) at Kayenta (elevation 1737 m [5700 ft]) to 9.8°C (49.7°F) at Navajo National Monument (elevation 2220 m [7285 ft]). Mean annual precipitation in northeastern Arizona is relatively low for the moderate elevations typical of the region (Sellers and Hill 1974), and for this reason the area has been called a "rainfall sink" (Brown 1982). Mean annual precipitation at Kayenta is a scant 198 mm (7.78 in), and at Navajo National Monument it is 291 mm (11.46 in). Mean annual precipitation of seven sites (mean elevation 2054 m [6740 ft]) on the Peabody lease is 260 mm (10.22 in). This precipitation is bimodal, with nearly 46% falling as convectional showers in July, August, and September. The remainder falls throughout the year as cyclonic rain and snow. January and June are the driest months. The dry climate allows only intermittent perennial stream flow. Ephemeral flows may result from thunderstorms and melting snow. Prevailing winds are southwesterly. May and June frequently have warm, dry winds that add to the approximately 1015 mm (40 in) annual evaporation rate.

Habitats and Associated Birds

Fourteen habitat types have been identified for this report and are mapped in Figure 3. Designation of a particular habitat is based on one or more of the following: perennial plant species composition, vegetative physiognomy, topographic uniqueness, and distinctiveness of the associated breeding bird species composition. The sequence of the presentation of the habitats follows increasing breeding bird species richness, which is considered here to be an approximation of breeding bird species diversity (see Ralph 1985, Brotherson et al. 1981, Wiens and Rotenberry 1981). Tables are also arranged by this sequence. Habitats in the study area may be sharply demarcated as in ponds, riparian areas, or cliff scarps. As a rule, however, there is much interspersion between them.

Breeding bird communities of northern Black Mesa comprise a complex of species derived principally from the Sonoran and boreal faunal areas, utilizing a series of plant communities of Great Basin origins. (Faunal derivations of native terrestrial breeding birds of northern Black Mesa follow Behle [1985]). The upland nature of the study site may explain the high number of boreal species (44%), while the geographic position of the area in the southwestern United States probably accounts for the similar proportion of Sonoran derivatives. Predominant habitats on northern Black Mesa are pinyon-juniper woodland and sagebrush, saltbush, and greasewood shrublands (Fig. 3), which are primarily Great Basin–derived plant communities (Brown 1982). However, only 9 birds of Great Basin origins are present on Black Mesa because the Great Basin is characterized by few endemic bird species (Behle 1985). Nearly 38% of boreal species and 57% of Sonoran species breed in these Great Basin–type habitats. Half of the 10 breeding species designated as typical of the pinyon-juniper woodland are derived from the Great Basin.

Montane Scrub

The montane scrub on Black Mesa is best developed on slopes of the outer mesa escarpment where conifers have not yet invaded rockfalls, slides, and slumps (Fig. 4). Because of this, montane scrub habitat may often be a seral stage of succession. Its establishment in an old burn of several hectares in mixed-

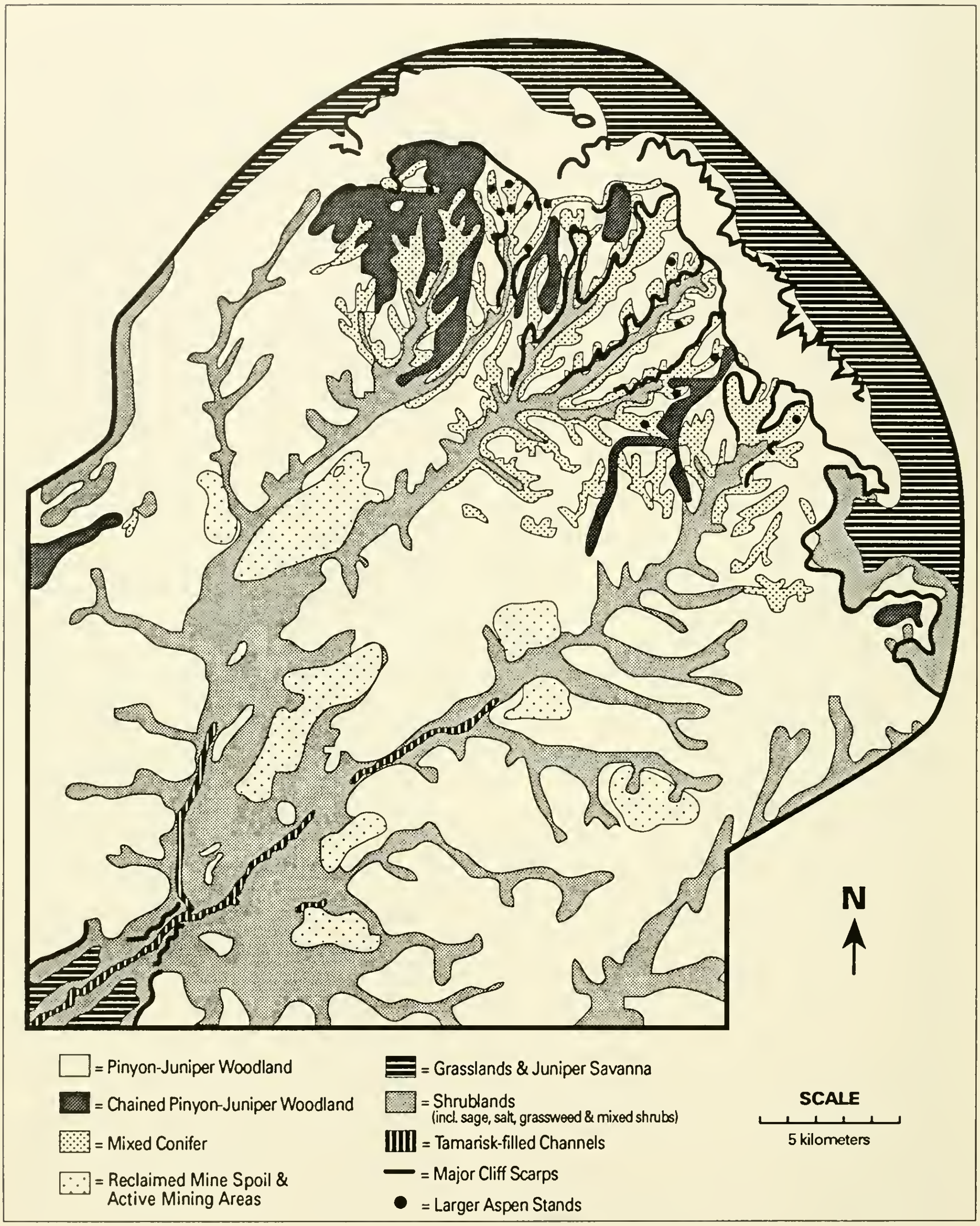
= Pinyon-Juniper Woodland
= Chained Pinyon-Juniper Woodland
= Mixed Conifer
= Reclaimed Mine Spoil & Active Mining Areas
= Grasslands & Juniper Savanna
= Shrublands (incl. sage, salt, grassweed & mixed shrubs)
= Tamarisk-filled Channels
= Major Cliff Scarps
= Larger Aspen Stands
N
SCALE
5 kilometers

Fig. 3. Vegetative communities of northern Black Mesa.

conifer woodland in upper Moenkopi Wash indicates such a condition. It occurs from 2133 to 2470 m (7000 to 8100 ft) and is distributed extensively east of the study site along the northern face of Black Mesa. The dominant species of this habitat include Gambel oak (*Quercus gambelii*), snowberry (*Symphoricarpos* sp.), cliff fendler bush (*Fendlera rupicola*), wax currant (*Ribes cereum*), Utah serviceberry (*Amelanchier utahensis*), wild-rose (*Rosa*

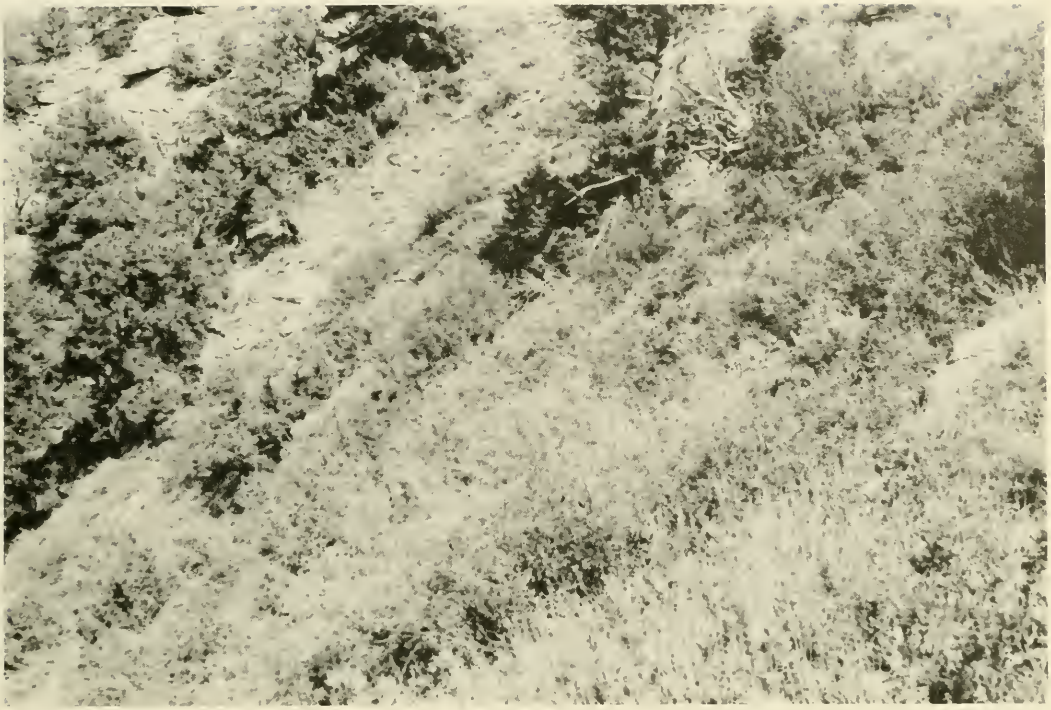

Fig. 4. Montane scrub below Lolomai Point, August 1987.

arizonica), and skunkbush sumac (*Rhus trilobata*). A deciduous shrubland has developed extensively in chained pinyon-juniper woodland on Lolomai Point.

Five bird species, dominated by ground-nesting and foliage-gleaning forms, are known to breed in montane scrub in the study area (Tables 1, 2): Scrub Jay, Orange-crowned Warbler, Virginia's Warbler, MacGillivray's Warbler, and Rufous-sided Towhee. No breeding densities have been determined in this habitat on Black Mesa. In Gambel oak–mountain mahogany and scrub oak–mountain mahogany scrub in Colorado, the number of species per plot varied from 9 to 18, with breeding densities of 53–116 individuals/40 ha (American Birds 1982, 1983). Rufous-sided Towhees and Scrub Jays were present in both habitats in both years. Brown (1982) considers the Virginia's Warbler and Rufous-sided Towhee to be characteristic of this habitat.

Sagebrush Shrubland

The sagebrush shrubland is dominated by big sage (*Artemisia tridentata*) to densities of approximately 10,870 shrubs/ha (4400/ac). Understory associates include blue grama (*Bouteloua gracilis*) and squirrel-tail (*Sitanion hystrix*) and a variety of forbs (Fig. 5). Pure sagebrush covers the deeper alluvial soils of the large valleys such as White-house Valley (Fig. 5), Reed Valley, and Coal Mine Wash, and canyons and basins at elevations of 1920–2377 m (6300–7800 ft).

Wintering and migrant bird species are characteristically sparse. All breeding species are ground-feeders, most of which are summer residents (Tables 1, 2). Bushtits forage frequently in sagebrush in winter, and Bewick's Wrens move into this habitat in late summer. Breeding species are the Horned Lark, Sage Thrasher, Green-tailed Towhee (restricted to Lolomai Point), Brewer's Sparrow, and Sage Sparrow, all of which are typical of sagebrush shrublands (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981). Overall spring densities are about 75 individuals/40 ha. Late-summer densities may reach 100 individuals/40 ha (Table 3). Rotenberry and Wiens (1980) report breeding densities in *Artemisia*-dominated shrubsteppe of 56–182.3 individuals/40 ha. Three to five species were found breeding on each plot. Two sagebrush plots in California supported six breeding

TABLE 1. Breeding bird community structure (nest site habitats) on northern Black Mesa, Arizona.

Habitat	Number of breeding species	Proportion of permanent residents	Nesting site substrate (proportion of species utilizing) Ground	Foliage	Cavity	Ledge	Diversity[a]
Montane scrub	5	0.40	0.80	0.20	—	—	0.501
Sagebrush	5	0.20	0.40	0.60	—	—	0.673
Saltbush	5	0.20	0.40	0.60	—	—	0.673
Greasewood	6	0.17	0.17	0.83	—	—	0.456
Reclaimed mine spoil	7	0.29	0.57	0.43	—	—	0.683
Juniper savanna	8	0.25	0.25	0.75	—	—	0.347
Riparian habitats	9	0.22	0.22	0.78	—	—	0.527
Ponds	9	0.11	0.89	0.11	—	—	0.563
Chained pinyon-juniper	11	0.45	0.36	0.28	0.36	—	1.092
Mixed-shrub	12	0.25	0.25	0.58	—	0.17	0.964
Aspen groves	14	0.36	0.36	0.36	0.21	0.07	1.238
Cliffs, talus, banks	20	0.50	0.05	—	0.40[b]	0.55	0.845
Pinyon-juniper	42	0.55	0.07	0.49	0.34	0.10	1.133
Mixed-conifer	59	0.58	0.12	0.45	0.29	0.14	1.247

[a] Diversity values derived using proportions of species utilizing each nesting substrate in Shannon-Wiener diversity formula (MacArthur and MacArthur 1961).
[b] Cavities in this situation to mean holes in cliffs or wash banks rather than in trees.

TABLE 2. Breeding bird community structure (foraging guilds) on northern Black Mesa, Arizona.

Habitat	No. breeding species	Foraging substrate/mode (proportion of species) Ground feeding	Aquatic feeding	Foliage gleaning	Bark gleaning	Nectar feeding	Sallying	Aerial	Predator/ scavenger	Diversity[a]
Montane scrub	5	0.20	—	0.80	—	—	—	—	—	0.501
Sagebrush	5	1.00	—	—	—	—	—	—	—	0.000
Saltbush	5	1.00	—	—	—	—	—	—	—	0.000
Greasewood	6	0.83	—	—	—	—	—	—	0.17	0.456
Reclaimed mine spoil	7	1.00	—	—	—	—	—	—	—	0.000
Juniper savanna	8	0.75	—	0.12	—	—	—	—	0.13	0.686
Riparian habitats	9	0.78	—	0.11	—	0.11	—	—	—	0.680
Ponds	9	0.44	0.56	—	—	—	—	—	—	0.735
Chained pinyon-juniper	11	0.56	—	0.18	0.18	—	—	—	0.08	1.145
Mixed-shrub	12	0.83	—	—	—	—	0.08	—	0.08	0.559
Aspen groves	14	0.14	—	0.57	0.14	—	—	—	0.14	1.145
Cliffs, talus, banks	20	0.15	—	0.10	0.05	—	0.10	0.20	0.40	1.583
Pinyon-juniper	42	0.19	—	0.31	0.07	0.02	0.10	0.07	0.24	1.702
Mixed-conifer	59	0.14	—	0.41	0.12	0.05	0.08	0.03	0.17	1.653

[a] Diversity values derived using proportions of species in each foraging guild in Shannon-Wiener diversity formula (MacArthur and MacArthur 1961).

species at total densities of 47 and 17 individuals/40 ha (American Birds 1979). Smith et al. (1984) reported breeding-bird densities of 61.2 and 65.2 individuals/40 ha in sagebrush in Idaho over a 2-year period.

Saltbush Shrubland

Saltbush shrubland habitat occurs as pure stands of fourwing saltbush (*Atriplex canescens*) in valleys on alluvial terraces at 1980–2070 m (6500–6800 ft). These stands are usually upstream from stands of greasewood (*Sarcobatus vermiculatus*). Cheatgrass (*Bromus tectorum*) and stickseed (*Lappula redowski*) frequently dominate the understory. Saltbush stands are well developed in the middle portion of Yellow Water Wash, in Reed Valley, and in portions of Dinnebito Wash (Fig. 6). Open stands grow in places at the foot of the mesa.

Like the sagebrush shrubland, the saltbush breeding bird assemblage is composed of ground-feeding, summer-resident species (Tables 1, 2). Bird densities in saltbush are

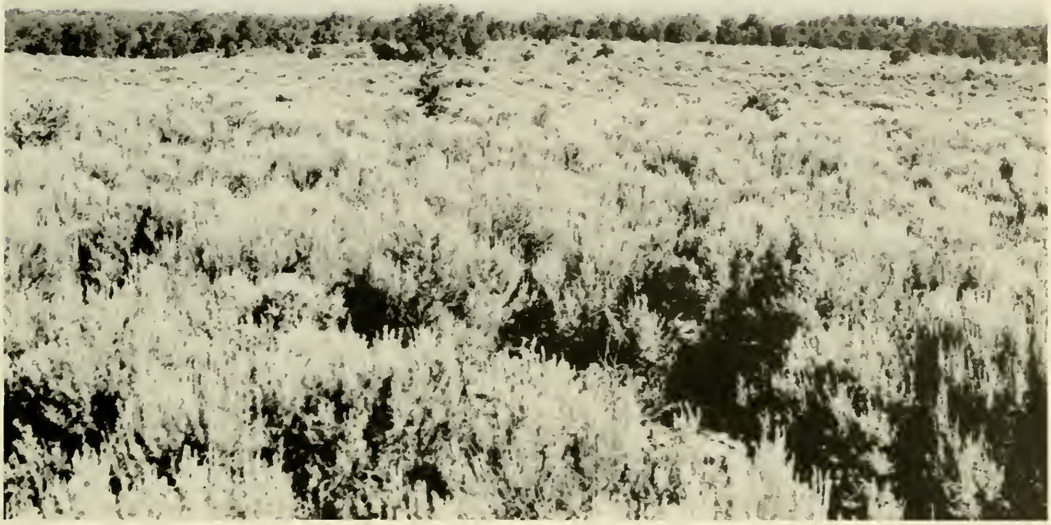

Fig. 5. Sagebrush shrubland, White House Valley, June 1987.

higher than those in sagebrush (Table 4). Mid-April 1982 densities in Reed Valley and Dinnebito Wash were 121 and 138 individuals/40 ha. The dominant breeding species is the Brewer's Sparrow. Four remaining breeding species are the Horned Lark, Sage Thrasher, Vesper Sparrow, and Sage Sparrow, although the latter species is sparse in saltbush as a breeding species. Of two saltbush plots (presumably *Atriplex canescens*) in California, one supported no breeding birds, the other six species at 21 individuals/40 ha (American Birds 1979). A third plot in shadscale scrub (*A. confertifolia*) supported five species at 30 individuals/40 ha (American Birds 1979).

Extensive grazing pressure in saltbush maintains an open understory that probably allows use of this habitat by Horned Larks. In

TABLE 3. Bird densities in two stands of sagebrush shrubland in the J-19 and J-21 mining areas[a].

	Bird density (no./40 ha)							
	Spring		Summer		Fall		Winter	
Species	J-19	J-21	J-19	J-21	J-19	J-21	J-19	J-21
Bushtit	—	10.6	—	—	—	—	—	—
Bewick's Wren	6.1	4.7	11.5	32.5	—	—	—	—
Blue-gray Gnatcatcher	—	—	9.4	5.3	—	—	—	—
Western Bluebird	—	5.3	—	—	—	—	—	—
Mountain Bluebird	5.6	13.3	8.2	4.5	3.5	—	—	—
Yellow-rumped Warbler	—	—	—	—	4.6	4.2	—	—
Brewer's Sparrow	27.5	—	38.2	8.9	—	8.0	—	—
Sage Sparrow	41.2	37.5	29.3	33.3	12.4	—	—	—
House Finch	—	—	—	15.4	—	—	—	4.4
TOTAL	80.4	71.4	96.6	99.9	20.5	12.2	—	4.4

[a]Study conducted by Peabody (1982–83).

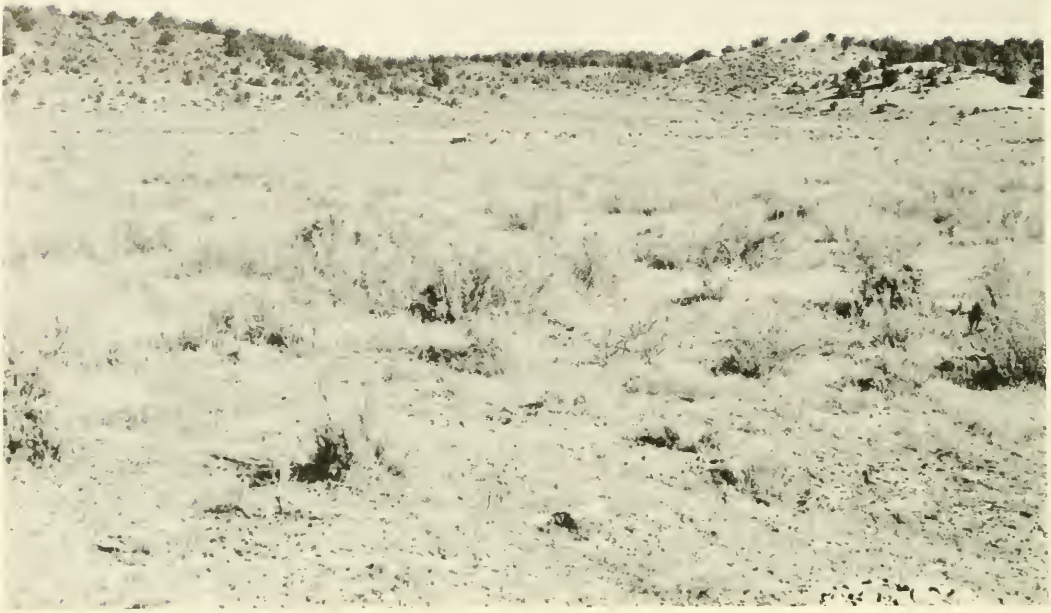

Fig. 6. Saltbush shrubland, Dinnebito Wash, June 1987.

winter, Horned Larks are the only species that can be considered common in saltbush.

Greasewood Shrubland

Greasewood shrubland dominates terraces of the larger and lower wash valleys of Moenkopi, Coal Mine, Yellow Water, Red Peak, and Yucca Flat washes (Fig. 7). It is typically found below 1920 m (6300 ft). Shadscale (*Atriplex confertifolia*), alkali sacaton (*Sporobolus airoides*), and cheatgrass are common understory associates.

The breeding bird species community of greasewood is dominated by summer-resident, foliage-nesting, and ground-feeding forms (Tables 1, 2). The Northern Mockingbird, Bendire's Thrasher, Loggerhead Shrike, Lark Sparrow, Brewer's Sparrow, and Black-throated Sparrow are known breeding species of greasewood. The greasewood stand censused in Table 5 shows significant numbers of Sage Sparrows and House Finches, but it is not known whether they nested in this particular higher-elevation (2042 m [6700 ft]) stand. The relatively large number of species recorded for this stand may be due to the presence of surface water in the arroyo that bisected it. Extensive greasewood stands on lower Moenkopi Wash have not been censused. Results of such work would probably be typical of shrubsteppe vegetation, with breeding bird densities around 60–180 individuals/40 ha comprising 3–5 species (Rotenberry and Wiens 1980), particularly those noted above. Bradfield (1974) found the Northern Mockingbird, Bendire's Thrasher, and Black-throated Sparrow to be characteristic of greasewood on Oraibi Wash at the southern edge of Black Mesa. I have found Sage Thrashers breeding in greasewood stands at Kayenta just outside the study area.

Reclaimed Surface Mine Spoil

Initiation of the large-scale surface coal mining operation by Peabody Coal Company in the 1960s saw extensive tracts of land undergo what is essentially a type conversion. By agreement with the Navajo and Hopi tribes, the postmining land use of the areas proposed for coal extraction was designated as livestock raising. Therefore, a grassland vegetation type best suited for effective livestock production is the objective sought in postmining reclamation efforts.

TABLE 4. Bird densities in two stands of saltbush shrubland in Reed Valley (RV) and Dinnebito Wash (DW)[a].

	Bird density (no./40 ha)							
	Spring		Summer		Fall		Winter	
Species	RV	DW	RV	DW	RV	DW	RV	DW
Say's Phoebe	24.0	8.8	—	5.7	—	—	—	—
Horned Lark	—	8.8	—	50.3	—	49.8	—	41.4
Rock Wren	9.8	3.5	9.6	7.3	—	—	—	—
Bewick's Wren	5.9	—	5.7	1.8	—	—	—	—
Sage Thrasher	8.6	19.5	—	—	—	—	—	—
Mountain Bluebird	5.3	16.9	2.9	4.5	—	7.8	—	—
Yellow-rumped Warbler	—	—	—	—	—	26.6	—	—
Brewer's Sparrow	23.1	10.0	84.7	163.2	—	—	—	—
Vesper Sparrow	—	27.5	—	—	—	14.8	—	—
Sage Sparrow	7.7	22.9	—	—	—	8.9	—	—
White-crowned Sparrow	—	—	—	—	134.8	57.4	—	—
House Finch	37.3	20.8	7.6	13.3	—	5.3	—	—
TOTAL	121.7	138.7	110.5	246.1	134.8	170.6	—	41.4

[a]Studies conducted by Peabody (1982–83).

To date about 4300 ha (10,625 ac) of regraded mine spoil has been seeded with grasses and other range plants (Fig. 8). Land that has been reclaimed lies between 1980 and 2072 m (6500 and 6800 ft); however, by the time mining is completed, some areas may lie above 2134 m (7000 ft) and about 8900 ha (22,000 ac) will be reclaimed. The mix of species planted for each area varies, but typical species used are crested wheatgrass, western wheatgrass, intermediate wheatgrass (*Agropyron intermedium*), various other

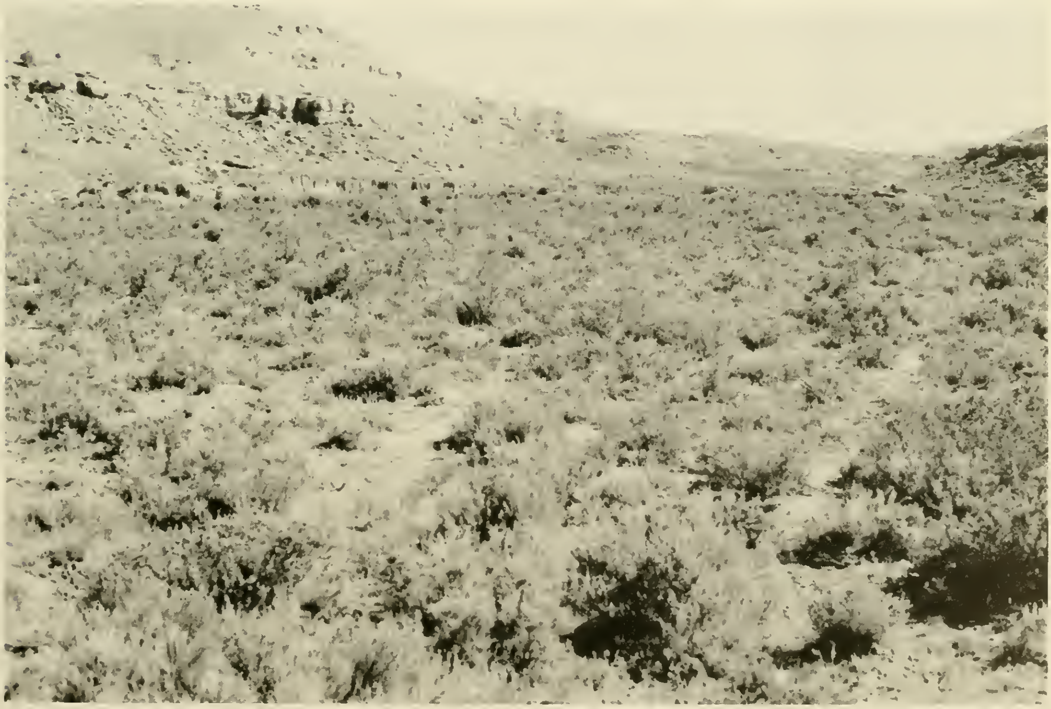

Fig. 7. Greasewood shrubland, Moenkopi/Red Peak Valley Wash confluence, June 1987.

TABLE 5. Bird densities in greasewood-saltbush shrubland in the J-28 mining area[a].

	Bird density (no./40 ha)			
Species	Spring	Summer	Fall	Winter
Rufous Hummingbird	—	2.2	—	—
Northern Flicker	—	1.8	2.7	0.9
Gray Flycatcher	—	8.0	—	—
Say's Phoebe	8.9	—	—	—
Ash-throated Flycatcher	6.7	—	—	—
Horned Lark	—	—	—	55.2
Scrub Jay	—	0.9	1.8	—
Mountain Chickadee	—	0.6	—	—
Bushtit	—	—	—	30.2
Rock Wren	11.1	0.9	2.7	—
Bewick's Wren	—	26.7	—	0.9
Mountain Bluebird	17.8	3.6	5.3	—
Solitary Vireo	—	4.4	—	—
Warbler	2.2	—	—	—
Chipping Sparrow	15.6	2.7	—	—
Brewer's Sparrow	—	7.1	—	—
Vesper Sparrow	6.7	—	—	—
Lark Sparrow	15.6	—	—	—
Black-throated Sparrow	8.9	5.3	—	—
Sage Sparrow	22.2	20.0	—	—
White-crowned Sparrow	3.6	—	—	—
Dark-eyed Junco	8.9	—	39.1	248.9
Sparrow sp.	15.6	3.6	3.6	—
Meadowlark sp.	—	0.9	—	—
Cassin's Finch	1.8	—	—	—
House Finch	37.8	18.7	6.2	1.8
Pine Siskin	—	—	33.8	—
Unidentified sp.	—	18.8	—	—
TOTAL	183.4	126.2	95.2	337.9

[a]Studies conducted by Peabody (1981–82).

wheatgrasses, Russian wildrye (*Elymus junceus*), smooth brome (*Bromus inermis*), saltbush, alfalfa (*Medicago sativa*), sweet clover (*Melilotus officinalis*), some blue grama (*Bouteloua gracilis*), and Indian ricegrass (*Oryzopis hymenoides*). Areas reclaimed after mining contain the best-developed grasslands in the study area.

The breeding bird community is composed entirely of ground-feeding forms, most of which are summer residents (Tables 1, 2). Horned Larks are the typical birds throughout the year in such areas (Table 6). Western Meadowlarks are common breeding birds within the study area only on reclaimed areas. Where saltbush is well established, Mourning Doves, Sage Thrashers, and Brewer's and Vesper Sparrows have been found nesting in reclaimed areas (Table 6). Maximum breeding densities under such conditions have been found as high as 33 pairs/40 ha.

Cody (1966) reported 3–4 breeding species to be typical of grasslands worldwide. Rotenberry and Wiens (1980) report 2–6 (average 3.8) in shortgrass prairie and 3–5 (average 3.8) in mixed-grass prairie. They found breeding densities in these types to be 81.6–132.8 and 40–126.4 individuals/40 ha, respectively. Therefore, the reclaimed areas on Black Mesa support breeding birds at densities comparable to natural grasslands elsewhere in North America. However, breeding bird species richness is lower than most grasslands. This may be related to the relative structural and floristic simplicity of the reclaimed areas (MacArthur 1964, Karr and Roth 1971, Tomoff 1974, Willson 1974, Roth 1976).

Juniper Savanna

Juniper savanna is a predominantly overgrazed grassland terrain at the lowest edge of the pinyon-juniper woodland (Figs. 1, 10). It is located as a band at the foot of the mesa from 1770 to 1860 m (5800 to 6100 ft). Juniper invasion into grasslands has occurred in the southwestern United States in the past 130

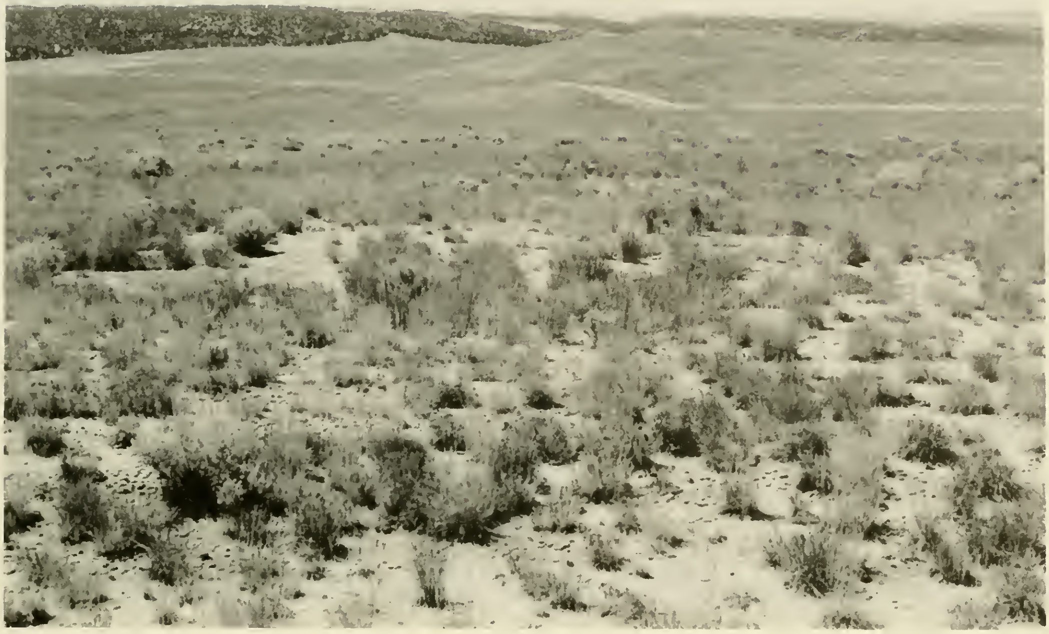

Fig. 8. Reclaimed mine spoil, N-2 reclaimed area, June 1987.

years (West et al. 1975); trees in this habitat, appearing relatively young, support this.

Vegetation is dominated by snakeweed, galleta, blue grama, squirreltail, Mormon tea (*Ephedra viridis*), narrowleaf yucca (*Yucca angustissima*), Indian ricegrass, sand dropseed (*Sporobolus cryptandrus*), and scattered Utah and one-seed junipers (*Juniperus osteosperma* and *J. monosperma*).

The majority of breeding species are summer-resident, foliage-nesting, and ground-feeding forms (Tables 1, 2). No censusing has been done in juniper savanna in the study area, but studies in similar habitats (Grue 1977, Beatty 1978 [both cited in Balda and Masters 1980]) indicated 11–23 breeding species/plot at densities of 35–179 pairs/40 ha. Since pinyon-juniper woodland on Black Mesa supports 68.5–106.7 pairs/40 ha (see Table 12), it seems reasonable to assume that breeding bird densities would be below 70 pairs/40 ha. Eight bird species are known to breed in juniper savanna in the study area: the Horned Lark, Northern Mockingbird, Bendire's Thrasher, Loggerhead Shrike, Chipping Sparrow, Lark Sparrow, Western Meadowlark, and Scott's Oriole.

TABLE 6. Spot-mapped breeding bird densities in three reclaimed areas in 1985 (no. pairs/40 ha).

	Reclaimed area		
Species	N-1	J-1/N-6	J-7
Mourning Dove	—	—	3.3
Horned Lark	19.2	17.7	16.3
Sage Thrasher	—	—	3.3
Brewer's Sparrow	—	—	3.3
Vesper Sparrow	—	+	3.3
Lark Sparrow	—	+	—
Western Meadowlark	—	2.2	3.3
TOTAL	19.2	19.9	32.8

+Present but density undetermined.

Riparian Habitats

Riparian habitats are the most restricted habitats in the study area. They are dominated by tamarisk (*Tamarix chinesis*) thickets that are usually less than 4.6 m (15 ft) tall. Fremont cottonwoods (*Populus fremontii*), although present as a few young individuals, are essentially absent from the study area. Russian olives (*Eleagnus angustifolia*) are actively advancing up Moenkopi Wash and are currently well established at about 1829 m (6000 ft). Dense

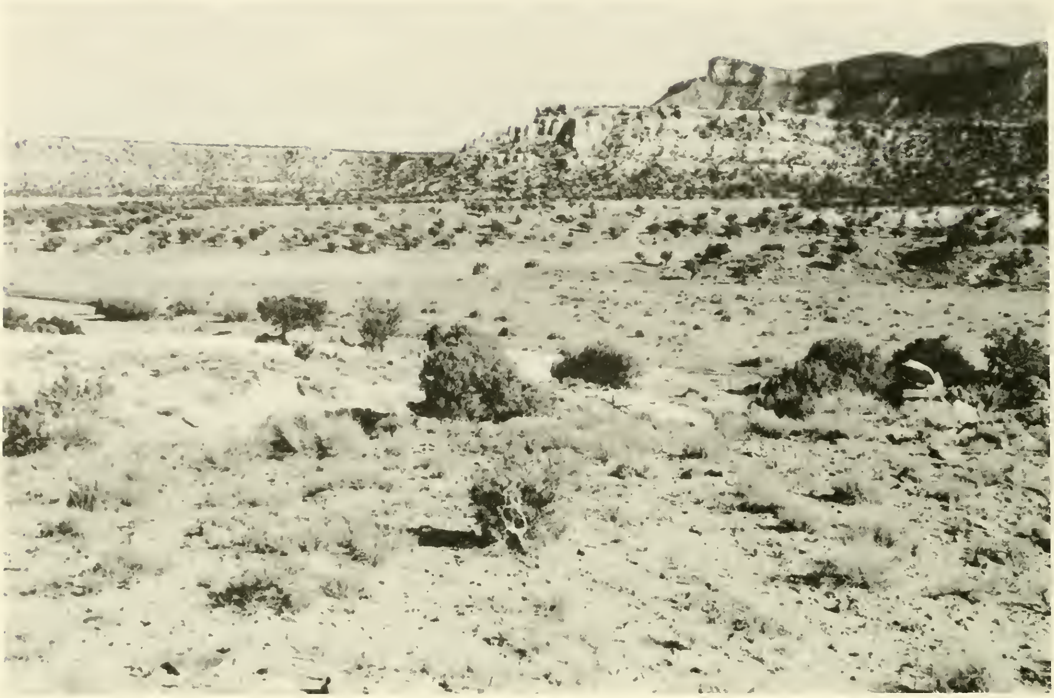

Fig. 9. Juniper savanna and the northern escarpment, Owl Spring Valley, June 1987.

tamarisk thickets grow on Coal Mine and Moenkopi washes (Fig. 9) below 1920 m (6300 ft). There is also a thicket at the confluence of Moenkopi Wash and Reed Valley at 1981 m (6500 ft). Tamarisk-filled wash channels are considered disclimax strand communities by Brown (1982). During the 1980s, tamarisk continued to establish and spread conspicuously throughout the study area. This perhaps indicates that its invasion has not yet ended.

Bird use of riparian habitats on Black Mesa, like that of ponds, is typified by heavy migrant use and few breeding species. Most breeding species are summer-resident, foliage-nesting, and ground-feeding forms (Tables 1, 2). The only species found nesting in tamarisk are the Killdeer, Scrub Jay, Bushtit, Blue Grosbeak, Lazuli Bunting, Indigo Bunting, and Brewer's Blackbird. The Black-chinned Hummingbird, House Finch, and Lesser Goldfinch are suspected breeders. Migrant densitites, usually much higher in fall than in spring (Table 7), averaged 666 individuals/40 ha from September to mid-October. Common fall migrants include the House Wren, Ruby-crowned Kinglet, Orange-crowned Warbler, Yellow-rumped Warbler, MacGillivray's Warbler, Wilson's Warbler, Green-tailed Towhee, Brewer's Sparrow, Chipping Sparrow, and White-crowned Sparrow. Wintering bird densities are dominated by Dark-eyed Juncos and White-crowned Sparrow. It is interesting that such numbers of insectivorous, foliage-gleaning migrants (nearly 68% of the total density) utilize tamarisk in the fall, while virtually no foliage-gleaning forms nest in it. An increase in arthropod densities may occur in late summer and fall, attracting migrants. However, Hunter et al. (1988) believe that insects do not limit insectivore use of tamarisk on the Colorado River in southwestern Arizona. Species from adjoining habitats, such as the Northern Mockingbird, Loggerhead Shrike, and Black-throated Sparrow, frequently forage in or near tamarisk. The Blue Grosbeak is a characteristic breeding species in tamarisk throughout the Southwest (Bradfield 1974, Jacobs 1986, Hunter et al. 1988). Dark-eyed Juncos and White-crowned Sparrows are common in tamarisk in winter in the southern edge of Black Mesa (Bradfield 1974).

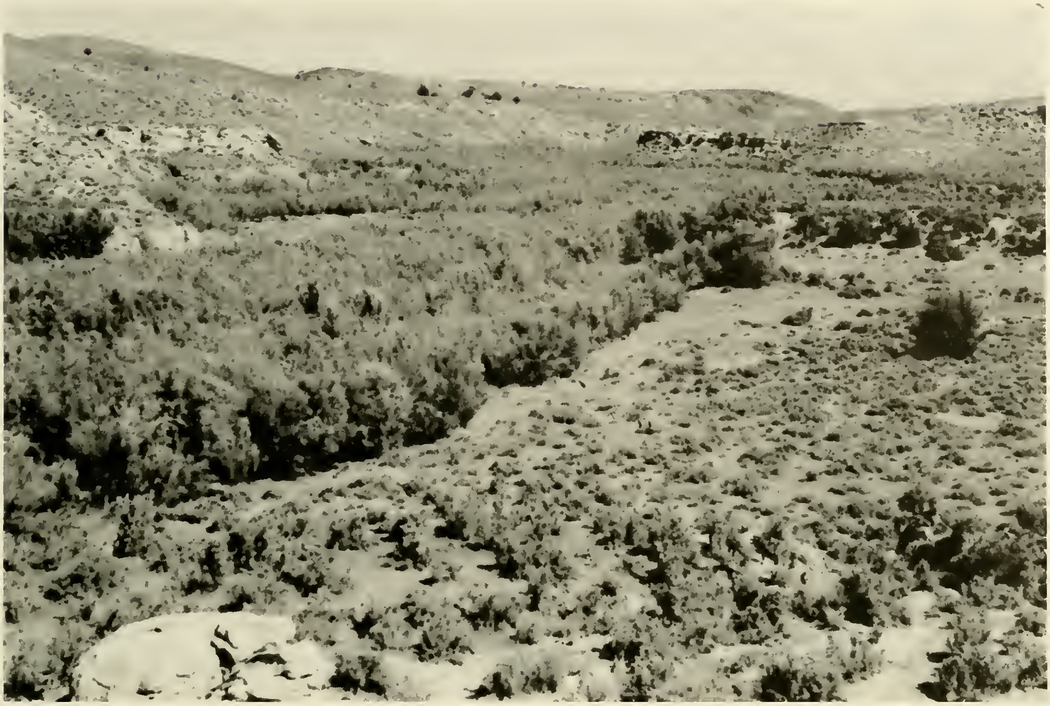

Fig. 10. Tamarisk thicket, Coal Mine Wash, July 1987.

Ponds

All ponds and standing water within the study area (over 150) are man-made. Older stock tanks were built by the Bureau of Indian Affairs, and nearly all recent ponds have been constructed within the Peabody lease area as required by surface mining environmental regulations. Some ponds exist in basins on reclaimed mine spoils. The extent of these ponds ranges from less than 1 ha (0.5 ac) to the nearly 12-ha (30-ac) J-7 pond (Fig. 11). Most are only a few hectares in size, and water persistence is usually temporary. Shoreline vegetation is often poorly developed because of heavy livestock grazing, the young age of most ponds, and fluctuating water levels. Tamarisk is the most frequent shoreline plant, although an occasional willow (*Salix exigua*) can be found. Emergent and aquatic vegetation includes cattail (*Typha* sp.), tules (*Scirpus* sp.), common poolmat (*Zanichellia*), sego pondweed (*Potamogeton*), and *Chara*. All ponds may freeze over during colder winter periods.

Most bird use of ponds is accounted for by migrant species (Peabody Coal Company 1984). Virtually all observations of the 32 species of waterfowl and 27 species of shorebirds seen on Black Mesa have been associated with ponds. Migrant swallows and blackbirds are frequently noted at ponds. Several species of sparrows utilize weedy pond edges while passing through during migration. Breeding is confirmed for seven species: Pied-billed Grebe, Mallard, Northern Pintail, American Coot, Killdeer, Brewer's Blackbird, and Red-winged Blackbird. Only the Mallard and Killdeer are frequent nesting species. Spotted Sandpipers may have nested at J-7 pond; Cinnamon Teal may also nest. All breeding species are summer residents, and most are ground-nesting forms (Tables 1, 2).

Chained Pinyon–Juniper Woodland

Mechanical elimination of pinyon-juniper woodlands was a widely followed type conversion practice to boost livestock production on southwestern rangelands. Most projects were conducted by various federal land-use agencies during the 1950s and 1960s when over 1.2 million ha (3 million ac) of woodland was eliminated (Lanner 1981). The specific technique

TABLE 7. Bird densities in tamarisk on Moenkopi Wash[a].

Species	Bird density (no./40 ha)[b]			
	Spring	Summer	Fall	Winter
Sharp-shinned Hawk	—	—	1.8	—
American Kestrel	—	7.2	—	—
Killdeer	7.2	7.2	—	—
Mourning Dove	1.8	—	5.4	—
Black-chinned Hummingbird	—	3.6	—	—
Hummingbird sp.	—	—	1.8	—
Red-naped Sapsucker	—	—	3.6	—
Downy Woodpecker	—	—	—	1.8
Northern Flicker	—	1.8	—	1.8
Hammond's Flycatcher	1.8	—	—	—
Gray Flycatcher	—	—	1.8	—
Say's Phoebe	—	3.6	5.4	—
Scrub Jay	3.6	—	—	1.8
Bushtit	—	—	1.8	—
Rock Wren	—	3.6	—	—
Bewick's Wren	—	—	12.6	9.0
House Wren	—	—	19.7	—
Ruby-crowned Kinglet	—	—	14.3	—
Blue-gray Gnatcatcher	—	—	7.2	—
Northern Mockingbird	3.6	3.6	—	—
Loggerhead Shrike	—	1.8	1.8	—
Warbling Vireo	—	—	1.8	—
Orange-crowned Warbler	1.8	—	50.2	—
Virginia's Warbler	—	1.8	—	—
Vermivora sp.	—	—	12.6	—
Yellow-rumped Warbler	3.6	—	591.9	—
MacGillivray's Warbler	—	—	28.7	—
Common Yellowthroat	1.8	—	5.4	—
Wilson's Warbler	—	—	48.4	—
Western Tanager	—	—	1.8	—
Blue Grosbeak	—	17.9	—	—
Lazuli Bunting	—	—	1.8	—
Green-tailed Towhee	—	—	28.7	—
Brewer's Sparrow	3.6	—	—	—
Spizella sparrows	—	—	226.0	—
Lark Sparrow	3.6	—	—	—
Black-throated Sparrow	—	1.8	—	—
Song Sparrow	—	—	1.8	—
Lincoln's Sparrow	3.6	—	—	—
White-crowned Sparrow	3.6	—	66.4	—
Dark-eyed Junco	—	—	—	191.9
Brewer's Blackbird	17.9	3.6	—	—
Brown-headed Cowbird	1.8	3.6	—	—
House Finch	—	—	3.6	—
Unidentified bird sp.	—	—	9.0	—
TOTAL	59.3	61.1	1155.3	206.3

[a]Based on single traverse of a 4460 × 50-m transect.

[b]Spring: 7 May 1987; summer: 25 June 1986; fall: 25 September 1986; winter: 21 January 1986.

used varied, but trees were usually uprooted by dragging naval anchor chain between two crawler tractors. The area was frequently seeded, usually with crested wheatgrass. Pinyon-juniper control has now fallen out of vogue for several reasons but primarily because of rising costs and poor cost-benefit ratios (Lanner 1981). However, it is still being done on northern Black Mesa, the most recent project completed in 1986.

All chained pinyon-juniper sites in the study area are on higher drainage divides and the mesa summit from 2165 to 2470 m (7100 to 8000 ft). The five sites are located as follows: (1) the mesa top where Navajo Route 41 crosses, (2) Lolomai Point, (3) the divide

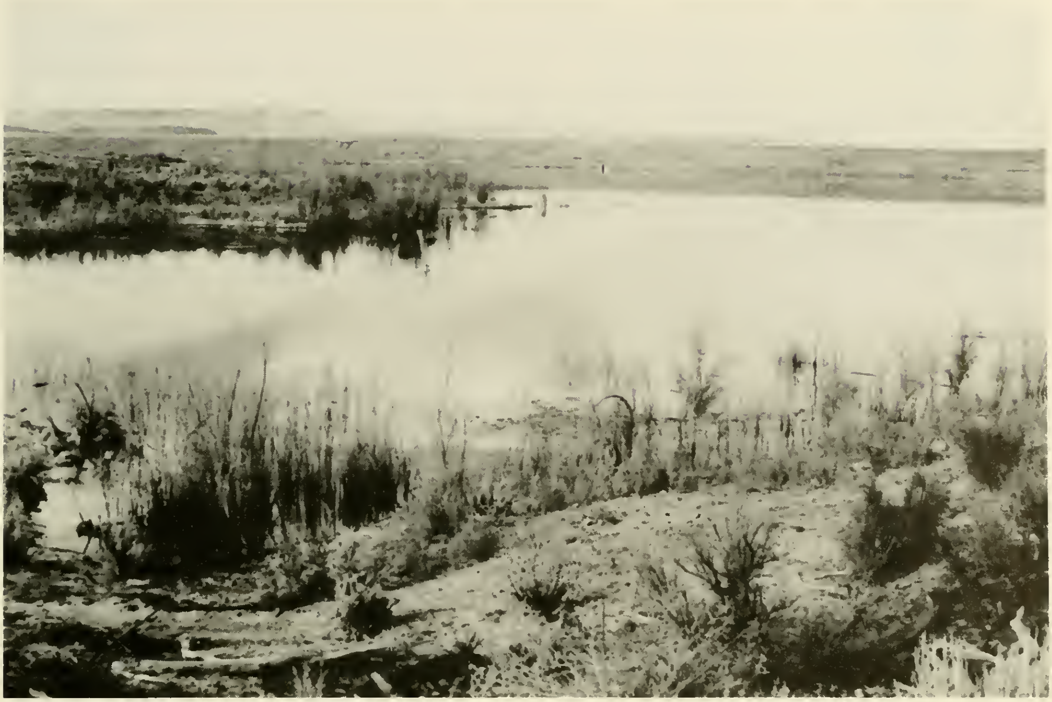

Fig. 11. J-7 Pond, June 1987.

between Yellow Water Canyon and the west fork of Coal Mine Wash, (4) about 2 km west of Kayenta Point, and (5) the divide between the east fork of Coal Mine Wash and Moenkopi Wash. These sites total about 3943 ha (9742 ac) (M. Roth personal communication to F. R. Vest). All five areas have been seeded with crested and western wheatgrass. The Lolomai Point chaining was conducted in 1972 (F. Vest personal communication). The remaining four sites were probably chained in the late 1960s or early 1970s.

The largest single site, Lolomai Point, has been and currently continues to be rapidly invaded by Gambel oak and Utah serviceberry (Fig. 12). The remaining sites are also being invaded by these shrubs, but the current density and stature of the plants are below that of Lolomai Point. Gambel oak occurs in a successional sequence with pinyon in Colorado (Floyd 1982). Although this appears to be the case on northern Black Mesa, it is probably happening only in the elevational range of the oak. During removal of the woodland, ponderosa pines (*Pinus ponderosa*) were left standing. The aspect created was that of meadows or clearings containing scattered large trees (Fig. 12).

About half of the 11 breeding species are permanent residents (Table 1). Cavity-nesting species are well represented along with foliage- and ground-nesting forms. A variety of foraging guilds are represented, but ground-feeding species comprise the majority (Table 2). Typical birds of chained areas are Lewis and Acorn Woodpeckers, Mountain Bluebirds, Rufous-sided and Green-tailed Towhees, and Chipping Sparrows. Red-tailed Hawks and American Kestrels readily use the isolated pines as perch sites. Further discussion of the effects of chaining on birds is presented on pages 33 and 34.

Mixed Shrubland

The mixed shrubland is an ecotonal vegetative association situated in the area where the major washes of the Moenkopi drainage converge (Fig. 13). Here, an open shrubland comprising big sage, black sage (*Artemisia nova*), saltbush, greasewood, shadscale, snakeweed (*Gutierrezia sarothrae*), and rabbitbrush (*Chrysothamnus greenei, C. nauseosus*) covers a landscape of hills and terraces. Grasses, primarily blue grama, galleta (*Hilaria jamesii*), and needle and thread (*Stipa comata*), are fairly well developed associates. Included in this

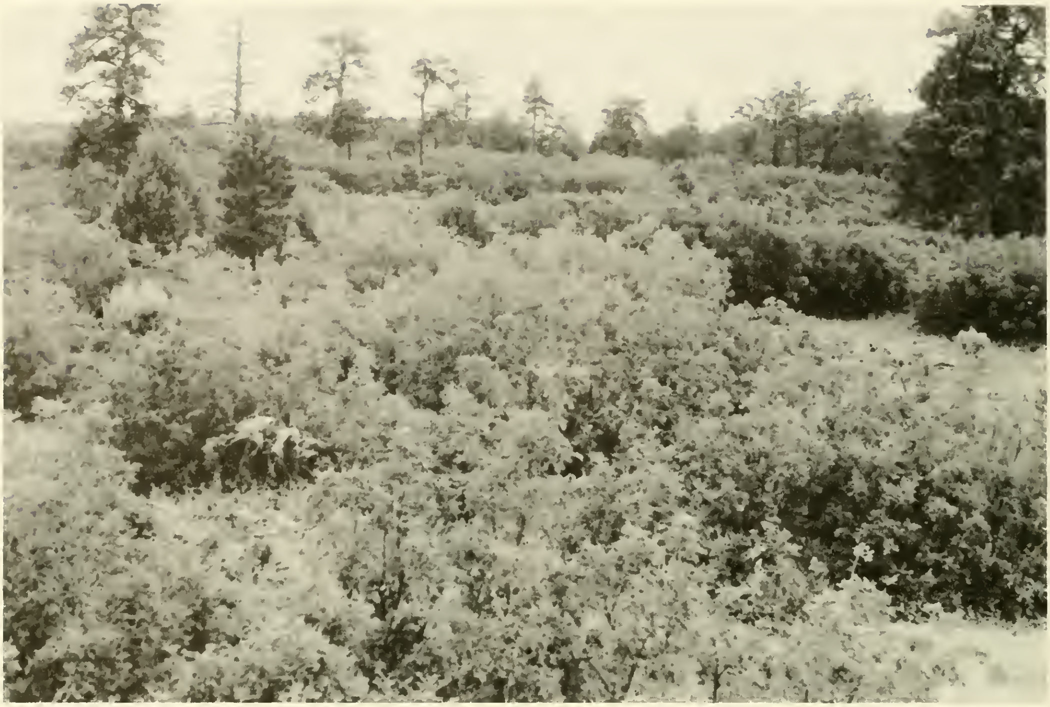

Fig. 12. Chained pinyon-juniper woodland invaded by Gambel oak, Lolomai Point, August 1987.

type are Mancos Shale slopes at the mesa foot and in the area of the Moenkopi Wash–Coal Mine Wash confluence that are covered with shadscale and Russian thistle (*Salsola iberica*). Elevations in this area are 1829–1980 m (6000–6500 ft).

Tomoff (1974), Wiens and Rotenberry (1981), and Smith et al. (1984) noted that certain desert scrub and shrubland bird species are associated with specific shrub species. Tomoff (1974) states that "plant species composition is highly significant in regulating breeding bird communities in desert scrub." Rotenberry (1985), in a study of grassland habitats, found that "over half (55%) of the variation in bird community composition was associated with floristic variation." Desert scrub bird communities in the study area support these statements, with several shrubland breeding birds being associated with particular shrub species. Sage Sparrows are most numerous in sagebrush, Sage Thrashers and Brewer's Sparrows prefer saltbush, and Black-throated Sparrows are typical of greasewood and shadscale. Because the mixed shrubland is a composite habitat, the breeding bird community composition at any particular site reflects the shrub species composition represented in it. For these reasons, any particular area of mixed shrubland typically supports more species of breeding birds than a monotypic shrubland (Tables 8, 9).

Shadscale occasionally occurs as nearly monotypic stands on exposures of Mancos Shale (or on the outwash fans of material eroded from the same). Such situations appear to support the lowest breeding bird densities and species richness of any of the native habitats on Black Mesa. Fautin (1946), Smith et al. (1984), and Medin (1986, 1990) examined bird communities in shadscale-dominated desert scrub in the Great Basin. Each study found about three species breeding at densities of 39.2–64.8 individuals/40 ha. Horned Larks were the most numerous species in each study, typically constituting the majority of total bird density.

The mechanism(s) of the relationship noted above are not clearly known. The tendency of some birds to nest in certain plant species (Tomoff 1974, Petersen and Best 1985) helps explain part of the relationship. Species-specific exploitation of arthropod faunas distinct to each shrub species may be important

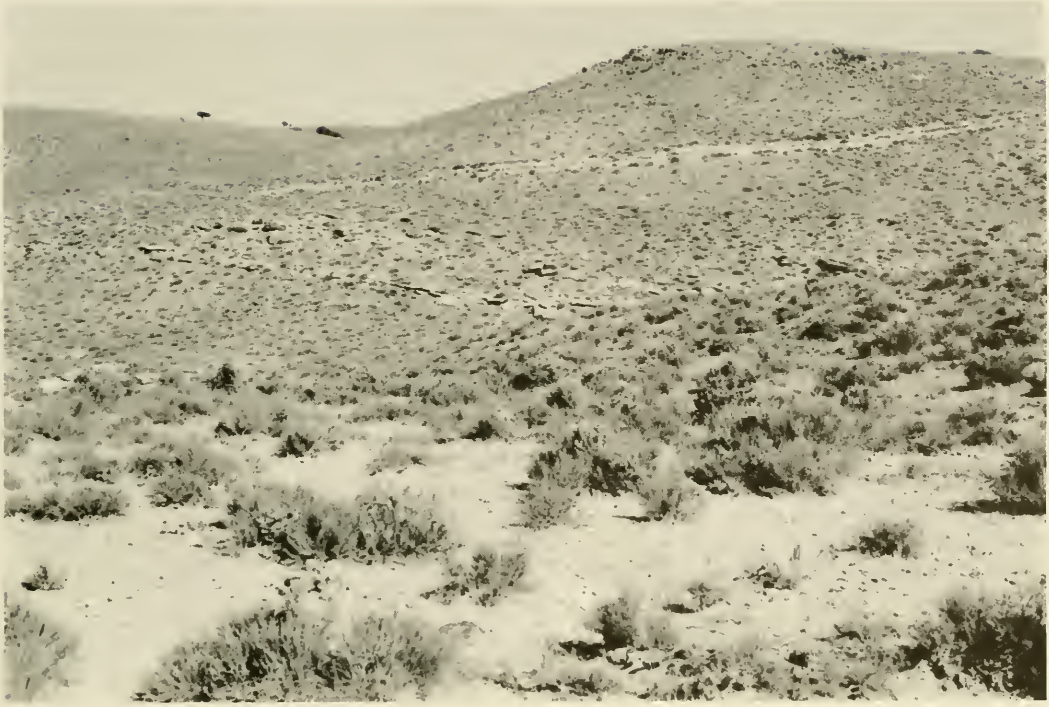

Fig. 13. Shadscale-dominated mixed shrubland, Moenkopi Wash, June 1987.

(Wiens and Rotenberry 1981). Rotenberry (1985) postulates that within similar habitat types "bird species/plant taxa associations . . . are mediated by the specific food resources that different plant taxa provide." Bird response to habitat physiognomy plays a key role in habitat selection and utilization (MacArthur 1964, Karr and Roth 1971, Wiens 1973, Willson 1974, Roth 1976). Shrublands on Black Mesa represent a single physiognomic type, with the shrub species comprising them all having Great Basin affinities (Brown 1982). It may be that the distinct bird species associated with various Great Basin desert scrub communities evolved through resource partitioning brought about by competitive interactions (Cody 1985).

Aspen Groves

Aspen groves are found in cool, moist heads of box canyons (Fig. 14) or sheltered ravines at elevations above 2195 m (7200 ft). These groves are dominated by quaking aspen (*Populus tremuloides*), box-elder maple (*Acer negundo*), Gambel oak, chokecherry (*Prunus virginiana*), and red osier dogwood (*Cornus stolonifera*). One grove contains several large narrowleaf cottonwoods (*Populus angustifolia*). Aspens, known from 39 sites within the study area, vary in stand size from a few trees to stands up to 1.86 ha (4.6 ac). Each major wash, except Dinnebito, contains aspen groves, but most are located in drainages of Yellow Water Canyon in the vicinity of Lolomai Point. Understory vegetation includes meadow rue (*Thalictrum fendleri*) and Oregon grape (*Berberis repens*). Poison ivy (*Rhus radicans*) and bracken fern (*Pteridium aquilinum*) are found in some areas. Cattle grazing has widely opened the shrub stratum in several groves, while in protected groves the understory may be nearly impenetrable.

Most of the 14 known or suspected breeding species in aspens are foliage-gleaning and ground- and foliage-nesting summer residents (Tables 1, 2). House Wrens and Warbling Vireos breed only in this habitat. No extensive censusing has been conducted in aspens on Black Mesa. The results in Table 10 suggest that rather high densities may occur. An aspen stand with scattered conifers in Colorado supported 30 species at 184 individuals/40 ha (American Birds 1979).

TABLE 8. Spot-mapped breeding bird densities in mixed shrubland near the J-7 mining area, 1984–86 (no. pairs/40 ha).

Species	1984	1985	1986
Mourning Dove	—	—	+
Say's Phoebe	1.5	—	2.1
Horned Lark	8.9	+	5.9
Northern Raven	—	—	+
Rock Wren	1.5	1.5	1.2
Mountain Bluebird	—	—	+
Northern Mockingbird	0.8	+	0.6
Sage Thrasher	+	—	3.0
Loggerhead Shrike	0.8	+	—
Brewer's Sparrow	3.0	8.9	7.4
Vesper Sparrow	+	+	—
Lark Sparrow	—	—	1.2
Black-throated Sparrow	11.9	5.9	8.9
Sage Sparrow	7.4	3.0	1.8
Brown-headed Cowbird	—	—	+
TOTAL	35.8	19.3	32.1
BREEDING SPECIES RICHNESS	8	4	9

+ Present but density undetermined.

Cliffs, Talus Slopes, and Wash Banks

Cliffs, talus slopes, and eroded wash banks are found at all elevations throughout the study site. On the outer mesa escarpment, the geologic strata that form cliffs are Dakota Sandstone, the Toreva Formation, and Yale Point Sandstone (Figs. 10, 15). Cliff heights in this area may be up to 107 m (350 ft), but are usually under 46 m (150 ft). Yale Point Sandstone is the cliff-former in canyons near the mesa rim. In the vicinity of the mine lease, the Wepo Formation rarely forms cliffs. Toreva Sandstone cliffs flank the valley where Moenkopi Wash exits the study area. Eroded wash banks are present throughout the study site where wash channels have dissected alluvial fill.

Twenty bird species are known or suspected to use ledges, or holes, in cliffs or wash banks as nesting sites. Several of these are restricted to such nesting sites in the study area and include the Prairie Falcon, White-throated Swift, Cordilleran Flycatcher, Violet-green Swallow, Northern Rough-winged Swallow, Cliff Swallow, Rock Wren, Canyon Wren, and Townsend's Solitaire. The majority are permanent residents, and aerial feeders and predators predominate (Tables 1, 2). Some require special conditions around suitable nesting sites; e.g., Cordilleran Flycatchers must also have mixed-conifer present and Northern Rough-winged Swallows have been found nesting only in holes in wash banks.

Pinyon-Juniper Woodland

Pinyon-juniper woodland (Fig. 16) is one of the most widespread communities in the southwestern United States, occurring where

TABLE 9. Bird densities in sagebrush–mixed shrubland near the J-7 mining area[a].

Species	Bird density (no. 40/ha)			
	Spring	Summer	Fall	Winter
Cooper's Hawk	—	—	—	1.4
Black-chinned Hummingbird	—	0.9	—	—
Hummingbird sp.	0.9	—	—	—
Say's Phoebe	—	0.9	—	—
Ash-throated Flycatcher	—	0.4	—	—
Horned Lark	17.8	10.1	109.3	186.7
Rock Wren	—	4.7	—	—
Western Bluebird	—	—	0.9	—
Bluebird sp.	—	—	0.4	—
Northern Mockingbird	—	0.4	—	—
Sage Thrasher	0.9	—	0.9	—
Brewer's Sparrow	2.7	0.6	—	—
Vesper Sparrow	0.9	—	—	—
Black-throated Sparrow	—	1.8	—	—
Sage Sparrow	—	4.4	2.7	—
Sparrow sp.	0.6	—	—	—
Western Meadowlark	—	—	1.8	—
Brewer's Blackbird	—	—	0.9	—
House Finch	0.4	—	—	—
TOTAL	24.2	24.2	116.9	188.1

[a]Study conducted by EH&A (1979–80) using Emlen transects.

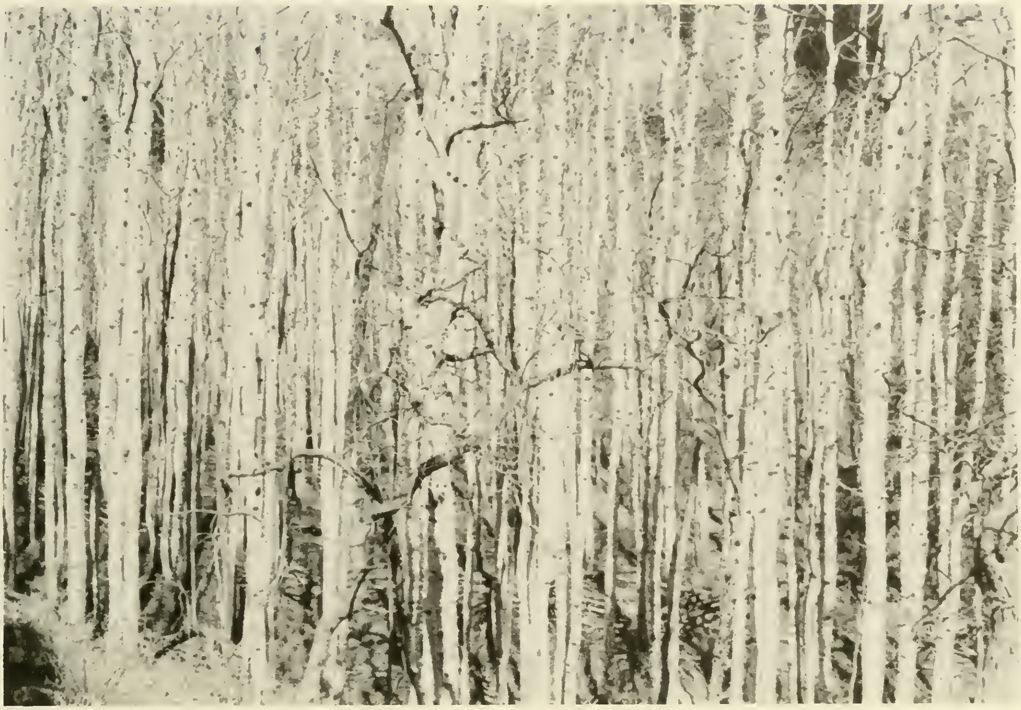

Fig. 14. Aspen grove, Moenkopi Wash, October 1986.

mean annual precipitation is 250–500 mm (9.8–19.7 in) (Brown 1982). It is the dominant plant community of Black Mesa (Fig. 3). The dark aspect this woodland imparts to the mesa when seen from a distance is said to account for the name "Black Mesa." Throughout Black Mesa, the woodland begins appearing at about 1830 m (6000 ft) and is found from this elevation to the mesa's highest reaches at over 2470 m (8100 ft).

Colorado pinyon (*Pinus edulis*) and Utah juniper are the principal trees of this woodland (Fig. 16). Junipers dominate at lower elevations, and as elevation increases, pinyons become dominant, total tree density increases, and trees become larger in stature (Table 11). Tree densities may exceed 400/ha near the mesa's northern rim. Understory is usually open but variable. In some places it is nearly bare, while in others big sage may be quite dense. Cliffrose (*Cowania mexicana*) and Gambel oak are frequently found in the woodland. Above 2200 m (7200 ft), cliff fendlerbush and antelope bush (*Purshia tridentata*) are common understory associates. Silverleaf buffaloberry (*Shepherdia rotundifolia*) is a common understory associate on the rocky mesa scarp and in canyons near the mesa rim. Manzanita (*Arctostaphylus pungens*) is present in the woodland in a few places near the mesa rim.

The assemblage of bird species at any point in the woodland is dictated by stand characteristics, tree density, tree species composition, and abiotic factors such as soil, slope, and exposure. No single area of woodland will support all of the 41 known or suspected breeding species. Several species breed in higher-elevation stands while others nest in the lower, open stands. Scott's Orioles, Gray Vireos, and House Finches are typical low-stand species. The Hairy Woodpecker, Mountain Chickadee, White-breasted Nuthatch, Solitary Vireo, Black-throated Gray Warbler, and Rufous-sided Towhee are most common in higher-elevation stands. Eleven species are widespread throughout the woodland and can be considered typical of it: Gray Flycatcher, Ash-throated Flycatcher, Pinyon Jay, Mountain Chickadee, Plain Titmouse, Bushtit, Bewick's Wren, Mountain Bluebird, Solitary Vireo, Black-throated Gray Warbler, and Chipping Sparrow. These species (excluding the jay) accounted for 80.1–92.8% of the total breeding bird density in the three stands censused

TABLE 10. Census results in aspens on northern Black Mesa[a].

Species	No. present	
Turkey Vulture	5	utilize nocturnal roost
Sharp-shinned Hawk	2	pair with nest
Red-tailed Hawk	1	noted overhead
Broad-tailed Hummingbird	4	
White-throated Swift	—	foraging above canopy
Downy Woodpecker	1	
Hairy Woodpecker	4	
Northern Flicker	3	
Dusky Flycatcher	2	
Cordilleran Flycatcher	2	
Violet-green Swallow	—	foraging above canopy
Steller's Jay	2	
Scrub Jay	2	
Mountain Chickadee	4	
Pygmy Nuthatch	1	
Brown Creeper	1	
House Wren	1	
American Robin	2	
Solitary Vireo	1	
Warbling Vireo	4	
Orange-crowned Warbler	3	
Virginia's Warbler	1	
Wilson's Warbler	1	
Black-headed Grosbeak	4	
Northern Oriole	1	
TOTAL SMALL FORMS	44	

[a]Census conducted in the middle fork of Coal Mine Wash on 25, 26 May 1986. Six traverses counting all individuals detected. Approximately 2 ha censused.

in 1983 and 1984 (Table 12). Half of the breeding species are foliage nesters, but cavity nesters are also well represented (Tables 1, 2). Ten percent of the species nest on the ground (Table 1). In the three stands censused above, foliage-nesting pairs constitute 42.9% of the total nesting pairs in the highest tree-density stand. Foliage nesting pairs make up nearly 50% in each of the other two stands. Nearly 87% of foliage nests and 87% of all cavity nests located in Black Mesa woodland have been in Utah junipers.

Balda and Masters (1980) found that breeding bird density increases with increasing tree density. On Black Mesa an average breeding density of 66.7 pairs/40 ha (1983 and 1984) used a stand containing 150 trees/ha (Tables 11, 12). In a stand of 283 trees/ha, an average of 93.4 pairs/40 ha was found for the same years. A density of 105 pairs/40 ha was determined for a stand of 380 trees/ha. Total breeding bird density showed a strong positive correlation with total tree density (r = .99). Additionally, pinyon density was positively correlated with densities of Gray Flycatchers, Mountain Chickadees, and Black-throated Gray Warblers. These results reflect those

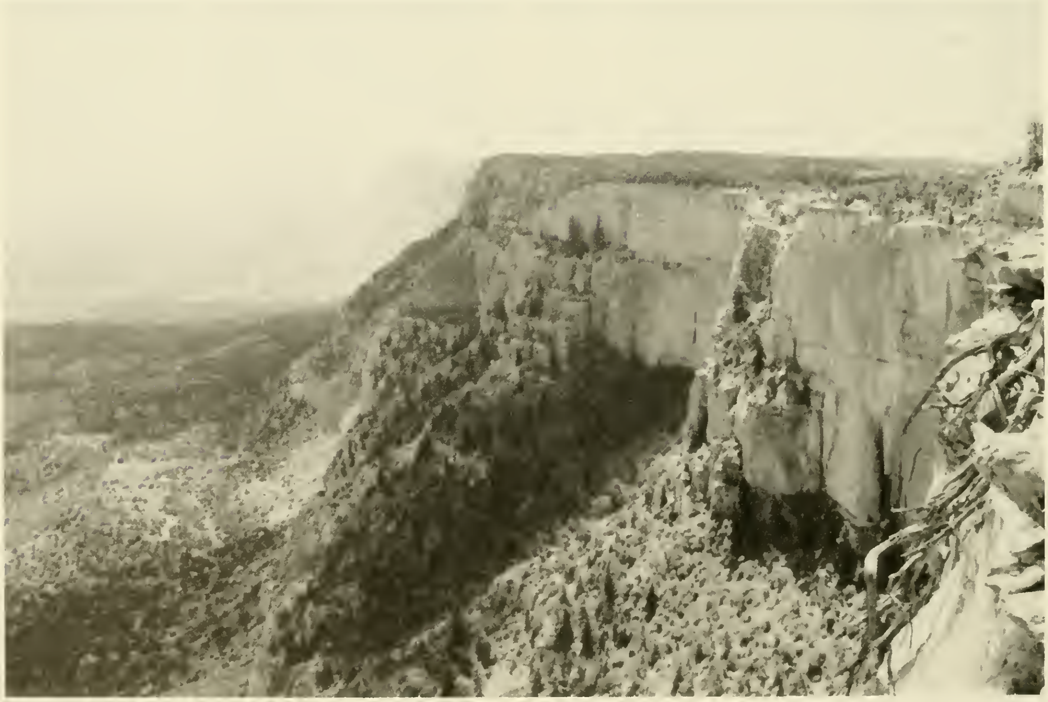

Fig. 15. Cliffs at the northern rim, September 1986.

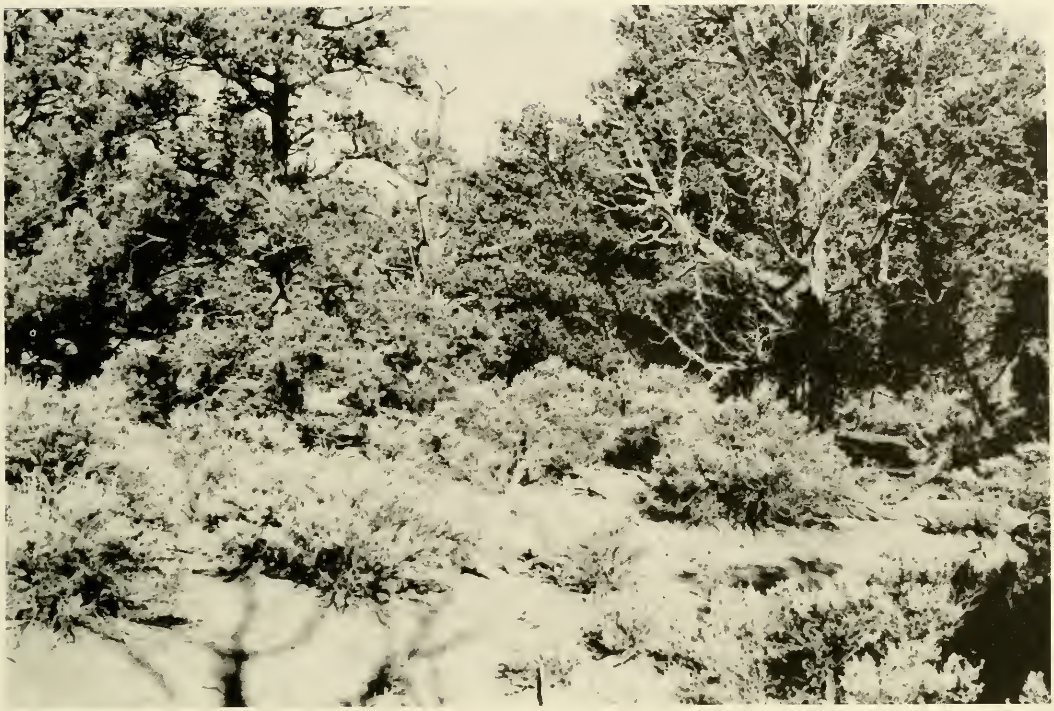

Fig. 16. Pinyon-juniper woodland, White House Valley, June 1987.

reported by Balda and Masters (1980), who also found Hairy Woodpeckers and White-breasted Nuthatches to be absent from stands with a pinyon-to-juniper ratio below 1:1. Sedgwick (1987) further quantified avian habitat relationships in pinyon-juniper woodland.

Results from Black Mesa are comparable to those of Balda and Masters (1980). They found that number of species per plot or study area from several studies varied from 12 to 24 (18 to 21 on Black Mesa). Breeding densities ranged from 30 to 190 pairs/40 ha and averaged around 95 pairs/40 ha. The average for Black Mesa plots is 88 pairs/40 ha. They noted that there may be large annual variations in overall breeding densities. The percentage of permanent residents appeared to be positively correlated with the proportion of pinyon pines and ranged from 35 to 53%. Large concentrations of robins, solitaires, and bluebirds that they report occurring frequently during winter in central Arizona woodlands have not been observed on northern Black Mesa.

Mixed-Conifer Association

The mixed-conifer association, found in the upper canyons and at sheltered cliff bases along the mesa rim (Fig. 3), occurs at 2070–2470 m (6800–8100 ft). It dominates the upper reaches of Yellow Water, Coal Mine, and Moenkopi washes and shallow drainages on the mesa summit near the rim (Fig. 17). A small, isolated stand occurs below the confluence of Reed Valley and Moenkopi Wash. Characteristic trees are Douglas fir (*Pseudotsuga menziesii*), ponderosa pine, and a pinyon-juniper woodland component of Colorado pinyon, Utah juniper, and rocky mountain juniper (*Juniperus scopulorum*). An isolated stand of white fir (*Abies concolor*) is present on Lolomai Point. Understory vegetation in mixed-conifer woodland is varied but typically includes Gambel oak, snowberry, cliff fendlerbush, mountain mahogany (*Cercocarpus intricatus*), and wax currant. Muttongrass (*Poa fendleriana*), western wheatgrass (*Agropyron smithii*), pine dropseed (*Blepharoneuron tricholepsis*), and mountain muhly (*Muhlenbergia montana*) are common understory grasses.

The "rainfall sink" situation of this region (Brown 1982) is reflected in the distribution of mixed-conifer and pinyon-juniper woodland habitats on the highest elevations of Black Mesa. Vegetative communities at similar

TABLE 11. Density and canopy cover of three stands of pinyon-juniper woodland on the Black Mesa leasehold.

	Site		
	J-10	J-20	J-21
Elevation	2012 m (6600 ft)	2103 m (6900 ft)	2164 m (7100 ft)
Total tree density	149.35/ha	282.80/ha	379.98/ha
Absolute density: pinyon	48.54/ha	141.40/ha	242.24/ha
Absolute density: juniper	100.81/ha	141.40/ha	137.74/ha
Proportion: pinyon	0.33	0.50	0.64
Proportion: juniper	0.67	0.50	0.36
Canopy cover (%)	10.61	13.37	26.16
Relative canopy cover (%): pinyon	31.90	49.15	69.07
Relative canopy cover (%): juniper	68.10	50.85	30.93
Mean tree height	4.02 m	3.66 m	5.00 m
Mean height: pinyon	3.9 m	3.52 m	4.93 m
Mean height: juniper	4.04 m	3.85 m	5.16 m

elevations to the south and west where rainfall is greater on the Mogollon, Kaibab, and Coconino plateaus are well-developed ponderosa pine or ponderosa pine–Douglas fir forest (Brown 1982). Mixed-conifer habitats occur on northern Black Mesa in specific areas where local abiotic conditions favor its development. These conditions all increase available moisture and are (1) deep, sheltered, and shaded canyons, (2) north-facing slopes, (3) joint traces and cracks where runoff is concentrated by bare exposures of Yale point sandstone, and (4) small, shallow drainages above 2255 m (7400 ft) where runoff is also concentrated. The pinyon-juniper woodland is still the dominant vegetation type on the broad mesa top (see Fig. 15) at elevations above 2440 m (8000 ft), indicating that the mesa's highest elevations probably receive no more than about 356 mm (15 in) mean annual rainfall. This is less than the 470–540 mm (18.5–21.3 in) reported for the above-mentioned uplands (Brown 1982) and approximates the isohyet estimate for northern Black Mesa by Cooley et al. (1969).

The mixed-conifer association supports the greatest richness of breeding bird species of all habitats present in the study area. Fifty-nine species are known or suspected to breed in mixed-conifer habitats (Table 1). Of these, nearly half are permanent residents. Foliage- and cavity-nesting forms predominate, although a variety of other nesting substrates are utilized by the remaining species (Table 1). Common characteristic breeding species include the Broad-tailed Hummingbird, Dusky and Cordilleran Flycatchers, Steller's Jay, Pygmy Nuthatch, Hermit Thrush, Grace's Warbler, and Dark-eyed Junco. Townsend's Warbler, along with MacGillivray's, Wilson's, and Orange-crowned Warblers, are common migrants. The Golden-crowned Kinglet is a typical winter resident. That Red-breasted Nuthatches may be common some winters is probably related to conifer cone crop irruptions (Widerlechner and Dragula 1984).

No bird density data have been collected in mixed-conifer woodland on Black Mesa. Breeding bird densities no doubt greatly exceed that of the pinyon-juniper woodland. A ponderosa pine stand on San Francisco Mountain, Arizona, supported 23 species at 232 pairs/40 ha, and a nearby mixed-conifer stand supported 27 species at 253 pairs/40 ha (Haldeman et al. 1973). A spruce-fir stand in the White Mountains, Arizona, supported 16 species at 169.7 pairs/40 ha and 17 species at 186.5 pairs/40 ha in two different years (Carothers et al. 1973). Franzreb (1977) reported mid- to late breeding season bird densities of 632.9 and 865.9 individuals/40 ha (31 and 40 species, respectively) in two consecutive years in unlogged White Mountain mixed-conifer forest. A logged stand supported 32 and 41 species at 544.0 and 758.0 individuals/40 ha, respectively, in the same two years. Brotherson et al. (1981) reported an early July density of 280 individuals/40 ha (26 species) in an aspen–mixed-conifer woodland in nearby Betatakin Canyon.

The mixed-conifer association and its bird species make northern Black Mesa unique. Most of the Navajo and Hopi reservations are dominated by arid deserts and semiarid grasslands, shrublands, and pinyon-juniper woodland. There are few montane "islands" rising

TABLE 12. Breeding bird densities[a] of three pinyon-juniper woodland stands on the Black Mesa leasehold (no. pairs/40 ha).

	J-10		J-20		J-30	
Species	1983	1984	1983	1984	1983	1984
American Kestrel	+	+	—	—	—	—
Mourning Dove	+	3.8	+	+	—	—
Common Nighthawk	+	—	+	—	—	—
Black-chinned Hummingbird	+	+	+	+	+	+
Hairy Woodpecker	+	+	+	1.9	+	3.8
Gray Flycatcher	7.6	7.6	7.6	11.5	11.5	9.5
Ash-throated Flycatcher	7.6	5.7	3.8	3.8	3.8	3.8
Scrub Jay	+	—	3.8	1.9	3.8	1.9
Pinyon Jay	+	+	+	+	+	+
Mountain Chickadee	3.8	3.8	7.6	7.6	11.5	9.5
Plain Titmouse	7.6	11.5	7.6	7.6	7.6	11.5
Bushtit	3.8	5.7	—	3.8	+	3.8
White-breasted Nuthatch	—	+	7.6	3.8	11.5	5.7
Rock Wren	+	—	—	—	—	—
Bewick's Wren	11.5	11.5	19.1	15.3	11.5	19.1
Blue-gray Gnatcatcher	—	+	3.8	—	3.8	3.8
Western Bluebird	—	—	+	—	3.8	3.8
Mountain Bluebird	3.8	1.9	3.8	7.6	3.8	—
Hermit Thrush	—	—	—	—	—	+
Solitary Vireo	3.8	1.9	7.6	3.8	3.8	3.8
Black-throated Gray Warbler	7.6	+	11.5	11.5	15.3	15.3
Rufous-sided Towhee	—	—	—	—	—	3.8
Chipping Sparrow	7.6	7.6	7.6	11.5	11.5	7.6
Black-throated Sparrow	+	—	+	—	—	—
Brown-headed Cowbird	+	+	+	+	+	+
House Finch	3.8	3.8	+	3.8	+	+
TOTAL DENSITY	68.5	64.8	91.4	95.4	103.2	106.7
TOTAL NUMBER OF SPECIES	21	19	21	18	19	20

[a] Spot-mapped, 1983–84.

+ Present but density undetermined because of insufficient data.

out of the dry lowlands. In the vast region bordered by the Little Colorado, Colorado, and San Juan rivers and the New Mexico state line, only Defiance Plateau, Navajo Mountain, and the Carrizo-Lukachukai-Chuska Mountain chain rise high enough to support extensive montane coniferous forests. The mixed-conifer woodland on Black Mesa is restricted and isolated but is sufficient to allow such montane species as Clark's Nutcrackers, Brown Creepers, Hermit Thrushes, and Yellow-rumped Warblers to breed within a few kilometers of the arid flats of Monument Valley.

Additional Discussion

The highest portions of northern Black Mesa support a rich association of montane breeding birds compared to other insular montane habitats in the Great Basin and Colorado Plateau. The mixed-conifer woodland alone supports 59 species, 32 of which are permanent residents. Johnson (1975) reported a mean of 37 species from a series of 31 montane islands in the Great Basin. The mean number of permanent resident species was 7.39. Behle (1978), in a similar analysis of 14 montane islands in Utah, had a mean of 42.7 species per island (17.0 permanent residents). All of those designated as "widespread species" (occurring on all islands) in both studies are known or suspected breeding species on Black Mesa. Both authors found the number of breeding species to be positively and significantly correlated with habitat diversity.

The remarkable breeding bird species richness on northern Black Mesa is related to the number and types of habitats occurring in the area. A well-documented concept in ecology states that increasing structural diversity of a plant community allows bird species diversity to increase (MacArthur and MacArthur 1961, MacArthur 1964, Karr and Roth 1971, Willson 1974, Roth 1976). If it is allowed that breeding bird species richness of a given habitat

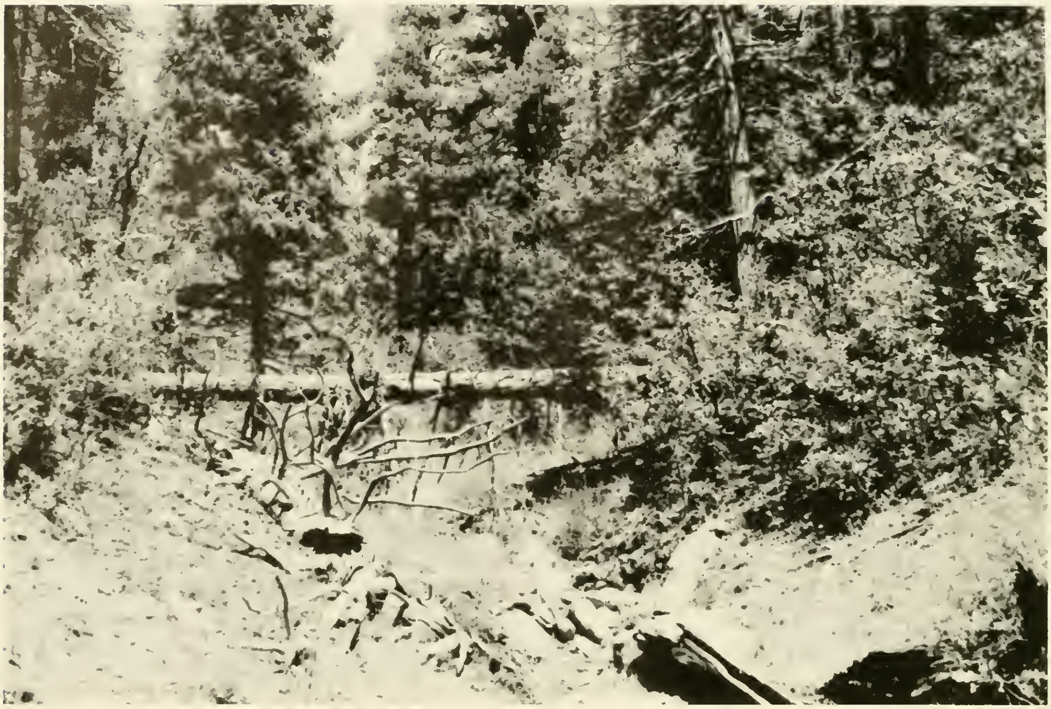

Fig. 17. Mixed-conifer woodland, Lolomai Point, August 1987.

corresponds to the breeding bird species diversity of that habitat, then a pronounced habitat complexity–breeding bird species diversity gradient is well illustrated on Black Mesa (Tables 1, 2). The structural simplicity of the scrub habitats allows utilization of them by fewer than 12 breeding bird species, with a given site generally supporting 3–4 species. The pinyon-juniper woodland bird diversity is far greater than the next nearest habitats. Mixed-conifer woodland supports the greatest diversity of breeding species for several reasons: greater stature and complexity, inclusion of the pinyon-juniper woodland component, and the relatively pristine decadent old-growth nature of portions of the habitat. Reclaimed mine spoil, juniper savanna, chained pinyon-juniper, and mixed-shrub habitats have higher species richness values than monotypic shrublands because each includes characteristics and/or plants species of other habitats.

Species richness of breeding bird associations of several habitats is surprisingly depauperate. Riparian habitats and ponds that are typically used by many bird species support only 7 and 9 breeding species, respectively. Factors responsible for this include the young age of the ponds, small size, isolated nature of both types, heavy livestock grazing in both types, and apparent inability of riparian breeding bird species to utilize the principal riparian plant species in the area, the exotic tamarisk. In pure montane scrub only 5 species are known to breed. In the relatively complex aspen groves, 14 species are known to breed. The small extent and isolated nature of the latter habitat probably prevent utilization of more species. The montane scrub, although appearing more complex than the Great Basin shrublands, is essentially a shrubland of restricted regional occurrence; again, isolation may prevent use by more species.

Faunal resemblance factors (Table 13) show limited overlap between breeding bird associations in the study area. Half of the pairs of habitats in Table 13 show no faunal resemblance (e.g., share no species). Approximately half of those pairs sharing species have factors below 0.21. The greatest resemblance factor is between sagebrush and saltbush shrublands (0.80), which probably reflects bird response to the very similar growth form of the two shrubs. Greasewood shrubland and juniper

TABLE 13. Faunal resemblance factors of the breeding bird communities of northern Black Mesa, Arizona[a].

	Montane scrub	Sagebrush	Saltbush	Greasewood	Reclaimed spoil	Juniper savanna	Riparian	Ponds	Chained pinyon-juniper	Mixed-shrub	Aspen groves	Cliffs, talus, banks	Pinyon-juniper	Mixed-conifer
Montane scrub	**5**	—	—	—	—	—	.12	—	.38	—	.32	—	.09	.13
Sagebrush	—	**5**	.80	.18	.50	.31	—	—	.25	.47	—	—	—	—
Saltbush	—	4	**5**	.18	.67	.15	—	—	.25	.47	—	—	—	—
Greasewood	—	1	1	**6**	.31	.57	—	—	.12	.67	—	—	—	—
Reclaimed spoil	—	3	4	2	**7**	.40	—	—	.22	.53	—	—	.04	.03
Juniper savanna	—	2	1	4	3	**8**	—	—	.11	.60	—	—	.08	.03
Riparian	1	—	—	—	—	—	**9**	.22	.10	—	—	—	.16	.06
Ponds	—	—	—	—	—	—	2	**9**	—	—	—	—	—	—
Chained pinyon-juniper	3	2	2	1	2	1	1	—	**11**	.18	.08	.13	.19	.14
Mixed shrub	—	4	4	6	5	6	—	—	1	**12**	—	.13	.04	—
Aspen groves	3	—	—	—	—	—	—	—	1	—	**14**	.06	.11	.30
Cliffs, talus, banks	—	—	—	—	—	—	—	—	2	2	1	**20**	.29	.20
Pinyon-juniper	2	—	—	—	1	2	4	—	5	1	3	9	**42**	.61
Mixed-conifer	4	—	—	—	1	1	2	—	5	—	11	10	31	**59**

[a]Resemblance factor (right of diagonal) follows Hoffmeister (1986) and is derived by doubling the number of species in common (left of diagonal) and dividing by the total number of species in each community (diagonal).

savanna have a resemblance factor of 0.57. This relatively high value is also probably related to bird response to structurally similar habitats. Principal plants in these habitats are larger, densely foliaged shrubs and small trees, respectively. The relatively high faunal resemblance factors of the juniper savanna and mixed-shrub (0.60), saltbush and reclaimed mine spoil (0.67), greasewood and mixed shrubland (0.67), and pinyon-juniper and mixed-conifer woodlands (0.61) are all related to similar habitat structure and/or floristic composition.

A few low faunal resemblance factors and their possible explanations are noteworthy. Pinyon-juniper and chained pinyon-juniper woodland have a resemblance factor of 0.19, reflecting the strong response of the breeding bird species composition to a pronounced physiognomic change. Furthermore, the value is this high because of four species that characterize the woodland edge and, therefore, utilize the openings created by chaining. Montane scrub shows no faunal resemblance with any of the Great Basin desert shrublands (sagebrush, saltbush, greasewood, and mixed shrublands). Although structurally similar, the lack of any faunal resemblance between these two shrubland types may be due to differences in their foliage growth form and geographical origins. The montane scrub is a high-elevation, cold-climate derivative (Brown 1982) of broad-leaved deciduous shrubs, while the Great Basin desert scrub communities are lower-elevation, desert-derived associations of sclerophyllous, often evergreen shrubs (Brown 1982). These differences are no doubt associated with the different avifaunas associated with each. Indeed, foliage gleaners comprise 80% of the breeding species in the montane scrub, and ground-feeding species comprise 78–100% of the species in the desert scrub habitats (Table 2). Ponds and riparian areas show a faunal resemblance only to each other, indicating a regional uniqueness of the associated breeding birds.

With increasing habitat diversity and accompanying breeding bird species diversity, there is also an increase in the number of different nesting site substrate and foraging substrate/mode guilds (Tables 1, 2). Ground- and foliage-nesting species are found in nearly all habitats. Cavity nesters, which utilize tree cavities, appear in tree-dominated habitats. Ledge nesters, logically, are dominant in cliffs, talus slopes, and wash banks. Ground-feeding species are found in all habitat types and comprise the principal guild in open, low-statured habitats. Foliage gleaners are prominent in the habitats composed of trees.

ENVIRONMENTAL CHANGES ON BLACK MESA

Environmental changes during the past 2000 years on the Colorado Plateau, and on Black Mesa in particular, have been well studied and documented. These changes have undoubtedly affected the avifauna of Black Mesa in many ways. The exact effect of many such changes on the bird life of the mesa, however, must remain conjectural. A brief discussion of several broad categories of change is presented below, along with comments on the effects such changes may have had on the birds of Black Mesa.

Climatic Changes

Climatic changes, speculated to be related primarily to changes in rainfall amounts, modes, or distribution, have been studied extensively in the Southwest (Euler et al. 1979). However, distribution of plant communities in the Black Mesa region has been minimally affected by such changes in the past 2500 years (Dean 1989). The principal effect of precipitation change has been in levels of alluvial water tables (Karlstrom 1983). Euler et al. (1979) postulate that a 550-year cycle of rainfall changes and the accompanying water table fluctuations are responsible for repeated aggradation and degradation of alluvial deposits along wash courses throughout the southwestern United States. They believe degradation, or arroyo cutting and gullying, follows lowered water tables during periods of low relative precipitation. Channels then refill with sediment as water tables rise during wetter periods.

Dean (1989) states that significant arroyo cutting episodes occurred on Black Mesa around A.D. 225–250, 750–775, and 1275–1300. Cutting of the present widespread gully network began around 1880–90 (Thornthwaite et al. 1942) and by 1915 had reached current conditions in the Polacca Wash drainage of eastern Black Mesa. Laguna Creek in neighboring Tsegi Canyon had gullied by at least 1918 (J. Wetherill unpublished letter to Talbot Hyde on file at American Museum of Natural History). Thus, in a period of only 25–35 years water tables lowered and alluvial valleys had been extensively dissected. Any riparian vegetation, particularly old cottonwood and willow growth, was probably drastically altered, if not eliminated, during this time.

The previous occurrence of native riparian habitats in the study area is conjectural. Three cottonwood posts identified from a large Anasazi site on Moenkopi Wash are associated with a structure dating to about A.D. 869–876 (Sink et al. 1983). Virtually no cottonwoods are present in the upper 39 km (24 miles) of Moenkopi Wash today. It is possible that a cottonwood-willow association was present in the vicinity of the Coal Mine and Moenkopi washes confluence where there are short reaches of perennial stream flow and dense, well-developed tamarisk thickets. Any cottonwood snags that may have existed after the cutting of the arroyo have disappeared. Karlstrom (1983) presents evidence that a series of small ponds occurred in Yellow Water Canyon at about 2073 m (6800 ft) elevation. Small ponds may have existed elsewhere, again, particularly along Coal Mine and Moenkopi washes. In 1896, Richard Wetherill reported ponds in the Tsegi Canyons similar to what may have occurred on a smaller scale in Yellow Water Canyon. The canyon had "two lagoons . . . from cliff to cliff about one mile apart and each one a mile long and about 300 yards wide. Ducks are plenty on these lakes" (R. Wetherill unpublished report on file at the American Museum of Natural History).

Bird species affected by the reduction or elimination of riparian habitats would include all species closely associated with these habitats throughout northeastern Arizona (see Woodbury and Russell 1945, Monson and Phillips 1981, and Hunter et al. 1987). Among these are the Western Kingbird, Yellow Warbler, Blue Grosbeak, Lazuli Bunting, Yellow-breasted Chat, and Northern Oriole. The disappearance of ponds would also have eliminated shorebirds and waterfowl and affected species characteristic of emergent vegetation such as the Marsh Wren, Common Yellowthroat, and Red-winged Blackbird. Bradfield (1974) discussed severe impacts of gullying on shorebirds and waterfowl on southern Black Mesa at Oraibi Wash. It is possible that the Black-billed Magpie, which disappeared from most of northeastern Arizona in the late 1800s (Woodbury and Russell 1945), was eliminated by alteration of riparian areas due to the current arroyo-cutting episode that began about the time of the bird's disappearance. Where this species does currently occur in extreme northeastern Arizona, it is associated with well-developed riparian growth (Jacobs 1986), indicating a dependence on such areas.

Several bird species typical of rock talus, cliffs, and ledges have moved to the exposed dirt banks along arroyos which exhibit attendant holes, caves, and crevices. Say's Phoebes, Northern Rough-winged Swallows, and Rock Wrens are characteristic of wash banks. American Kestrels, Great Horned Owls, Northern Flickers, Violet-green Swallows, and Mountain Bluebirds have been found to a lesser extent nesting in wash banks.

Exploitation by Prehistoric Man

Bird species identified from remains excavated from Anasazi archaeological sites are presented in Table 14. Excavation of these sites was conducted during the Black Mesa Archaeological Project (1968–83) as part of clearance procedures preliminary to mining operations by Peabody Coal Company. Six (39%) of the species identified were not found during this study (Table 14). It is striking that, as a group, Galliformes are so well represented. The Wild Turkey was obviously extensively utilized for a long period, and overuse by the Anasazi may have eliminated it from the area if it was not brought in as a domesticated species. The Scaled Quail may have been recently extirpated from the area by overgrazing (see below), but there are apparently no recent records of it for the region. Pat Ryan (personal communication), however, states that Scaled Quail are still present south of Black Mesa in the northern Hopi Buttes area. The Bobwhite may be a misidentification.

Raptors as a group are also well represented. The symbolism accorded raptors and their use by the Anasazi were probably similar to those by both present-day Hopi and Navajo. Rea (n.d.) indicates the broken and healed left radius and ulna of an immature Prairie Falcon from site AZ:D:7:98 are strong evidence that the bird was taken as a nestling and held in captivity. Several raptor species are currently taken from nests in the region by the Hopi (personal observation). Raptors have probably been used by Native Americans in this region nearly continuously for at least the last 1900 years. Periods of especially intensive use may

TABLE 14. Bird remains from Anasazi sites excavated during the Black Mesa Archaeological Project, 1968–83[a].

Species	No. sites	Approximate age(s)
Cooper's Hawk	2	A.D. 100–300, 800–1090
Red-tailed Hawk	3	A.D. 800–1090, 1100, 850–1150[b]
Buteo sp.	4	A.D. 600–1100, 850–975, 1100
Eagle sp. (*Aquila* or *Haliaeetus*)	3	A.D. 600–1100, 800–1030, 1070–1150
American Kestrel	2	A.D. 800–1030, 850–975
Prairie Falcon	1	A.D. 850–975
Wild Turkey[c]	20	A.D. 100–300, 800–1150
Northern Bobwhite[c]	1	A.D. 1100
Scaled Quail[c]	1	A.D. 1100–1150
Gambel's Quail[c]	1	A.D. 800–1090
Quail sp.[c]	1	A.D. 800–1030
Sandhill Crane[c]	1	A.D. 800–1090
Mourning Dove	1	A.D. 800–900
Screech Owl sp.	2	A.D. 100–300, 1100
Otus sp.	1	A.D. 800–1090
Great Horned Owl	3	A.D. 600–1100, 800–1030, 1100
Burrowing Owl[c]	1	A.D. 800–1030
Northern Flicker	3	A.D. 600–1100, 1100, one undated
Horned Lark	1	A.D. 100–300
Scrub Jay	2	A.D. 100–300, 600–1100
Pinyon Jay	5	A.D. 600–750, 600–1100, 850–975, 850–1150, 600–1100
American Crow	1	A.D. 850–975
Clark's Nutcracker	1	A.D. 600–1100
Common Raven	2	A.D. 850–975, 1100

[a] Based on the following reports: Olsen 1972, Rea n.d., Beezley 1974, Seme 1980, Seme and Harris 1982, Smiley et al. 1983, Nichols and Smiley 1984, Christenson and Perry 1985, and Leonard 1989.

[b] Anasazi occupation of northern Black Mesa ceased A.D. 1150 (Gummerman 1984).

[c] Not found on Black Mesa during this study, 1979–93.

have lowered the densities of some desirable or readily available species (e.g., Red-tailed Hawk and Golden Eagle). The Ferruginous Hawk was probably eliminated from the region by human exploitation (Hall et al. 1988).

Livestock Grazing

With their arrival in 1540, the Spanish introduced livestock to the Southwest. However, extensive use of livestock did not develop in the Black Mesa area until after 1868 (Thornthwaite 1942). Excessive overgrazing had, by the 1930s, become such a severe problem on the Navajo Reservation that a livestock reduction program was initiated by Collier in 1934–37 (Philp 1977). Overgrazing has brought about widespread changes in the bird life of Arizona (Phillips et al. 1964). Thornwaite et al. (1942) have cited it as a cause of excessive erosion and gullying in northeastern Arizona.

While Euler et al. (1979) believe arroyo cutting is a cyclic natural phenomenon associated with precipitation cycles, Thornthwaite et al. (1942) may be correct in concluding that overgrazing initiated the current arroyo-cutting episode. Under the influence of continued, heavy, year-long grazing and the successive replacement and supplanting of the relatively well-developed root systems of perennials with the shallow systems of weedy annuals, regional erosion will continue. As long as this situation remains, the cycle of alluvial aggradation and degradation may likely be eclipsed in its current state.

Grazing can have a significant impact on the plant community in which it occurs and in turn can affect the community's birds (Wiens 1973, Bock and Webb 1984). Wiens (1973) found that across a series of grassland types grazing caused "a uniform directional change towards dominance by plant species characteristic of drier climates." In addition to floristic changes in the community, grazing may produce marked physiognomic changes (Wiens 1973), such as reducing shrubs in riparian habitats (Taylor 1986) and increasing shrubs in grasslands (Phillips et al. 1964). Grazing can cause changes in the arthropod fauna of grasslands (Smith 1940), which could in turn cause a change in bird species composition (Wiens and Rotenberry 1981, Rotenberry 1985). Grazing has contributed to the spread of pinyon-juniper woodlands into grasslands during the past century (West et al. 1975). Grazing may cause changes in bird species composition with little change in overall bird density (Wiens 1973, Medin 1986), reduce bird species richness and density (Monson 1941, Wiens 1973, Taylor 1986), or even cause increases in density (Bock et al. 1984). Monson (1941) found that elimination of grazing and initiation of revegetation efforts in a grassland/shrubland site caused bird density to nearly double. Horned Lark densities increased on grazed grassland and shrubland sites (Wiens 1973, Bock and Webb 1984, Medin 1986). Western Meadowlark densities are reduced by grazing (Monson 1941, Wiens 1973). Bock and Webb (1984) and Bock et al. (1984) found Mourning Doves, Horned Larks, Mockingbirds, and Lark Sparrows to be significantly more numerous on a grazed grassland site than on an ungrazed site. The continuous, year-long grazing (by up to five species of livestock) typically practiced in the Black Mesa region has no doubt reduced prey species populations to the detriment of several species of raptors (Kochert et al. 1988).

Introduction of Exotic Vegetation

Plant species not native to the southwestern United States (or North America) are present in the Black Mesa region. Some arrived accidentally, while others were introduced for a variety of reasons. Species, both plant and animal, when introduced into a new region frequently increase rapidly in the absence of controlling factors with which they evolved in their native regions. Great disruptions in the numbers and composition of native flora and fauna can result where exotic species achieve dominance. The most conspicuous exotics within the study site are tamarisk (*Tamarix chinensis*), Russian thistle (*Salsola iberica*), and cheatgrass (*Bromus tectorum*). Other species include Russian olive (*Eleagnus angustifolia*), Siberian elm (*Ulmus pumila*), filaree (*Erodium cicutarium*), chorispora (*Chorispora tenella*), and summer cypress (*Kochia scoparia*).

The greatest impact of exotics on the bird life of the mesa probably occurs in riparian habitats and in grasslands. It is in such habitats that exotics are most conspicuous and dominant. Tamarisk is widely established along nearly all major washes in the region. Most stands have spread and grown up through natural dispersal, but in some places the species was planted by man, as at Keams Canyon (G. Monson personal communication). Preferential grazing of young cottonwoods and willows by livestock helps contribute to the monotypic tamarisk stands typical of the study area. On Black Mesa it is well developed along lower reaches of the major washes (see above).

In this region few breeding birds of native (cottonwood-willow) riparian stands breed in tamarisk. Migrant species forage extensively in tamarisk, and a few species, especially Dark-eyed Juncos, winter in it. Russian olive, also planted extensively in nearby areas, is dispersing rapidly in riparian habitats in the Intermountain West (Knopf and Olson 1984). Russian olives are currently well established and advancing up Moenkopi Wash below the confluence with Coal Mine Wash. Breeding bird use of mature Russian olive stands is limited, but winter use of fruits is extensive (B. Jacobs personal communication concerning stands in the Chinle Valley and personal observation at Keams Canyon; unpublished Black Mesa data). Tamarisk-dominated riparian strands in the study site support few riparian breeding obligates (e.g., Western Kingbirds, Yellow-breasted Chats, orioles, and buntings) but are intensively used by insectivorous migrants. As the Russian olive grove on Moenkopi Wash matured during the 1980s, numerous species appeared during winter, relying on the fruit as a food source. These species included Downy Woodpeckers, flickers, ravens, Mountain Bluebirds, robins, starlings, Cedar Waxwings, Yellow-rumped Warblers, White-crowned Sparrows, and Evening Grosbeaks.

Grassland habitats and disturbed sites in the study area are frequently composed of several exotic plant species. Effects on bird life in the study area are poorly known. It can be assumed, however, that there have been alterations in numbers, kinds, and distributions of grassland birds as a result. Cheatgrass is prevalent in juniper savanna at the mesa foot, and especially in saltbush stands. Russian thistle occurs abundantly on disturbed sites and is frequent on Mancos Shale slopes. Summer cypress is abundant early in the reclamation process. Horned Larks and Dark-eyed Juncos may feed extensively on Russian thistle and summer cypress during the winter, particularly following storms when these plants are the only abundant food source protruding above the snow.

Pinyon-Juniper Type Conversions

The purpose, methods, results, and areas of pinyon-juniper control on the study site were discussed previously. In any type conversion, the effect on wildlife must be considered radical. Impacts are especially pronounced when a woodland physiognomy is converted to that of a grassland or simple shrubland. In the case of birds, a nearly complete change in the composition of species occurs. In any particular converted site most woodland obligates are eliminated, and grassland and shrubland species invade the newly created openings. A few species absent or sparse in surrounding habitats may find favorable conditions in converted areas and experience population increases.

Bird species typically eliminated from woodland stands that have been converted on the study site include the Hairy Woodpecker, Gray Flycatcher, Mountain Chickadee, Plain Titmouse, White-breasted Nuthatch, Bewick's Wren, Blue-gray Gnatcatcher, Solitary Vireo, and Black-throated Gray Warbler. The majority of the above species are inhabitants of higher-elevation woodland stands where most conversion projects were conducted. Virtually all cavity-nesting species are eliminated. The effect of chaining on the Spotted Owl may be especially severe, particularly in the Lolomai Point area where the woodland was eliminated on the mesa tops adjacent to numerous small, mixed-conifer–filled canyons.

Several species characteristic of grasslands and shrublands and of woodland edge invade or increase as a result of woodland conversions. Chipping and Vesper Sparrows have invaded several chained sites in the study area. Mountain Bluebirds are common in chained sites, especially on Lolomai and Kayenta points. This open-area species probably increased in these areas while Western Bluebirds, a species typical of higher, dense stands, was reduced in numbers. In older chained areas where Gambel oak is established (see Fig. 12), Rufous-sided Towhees have increased. The Green-tailed Towhee breeds in the study area primarily where invading oaks are established on Lolomai Point. This area has also been colonized by Virginia's Warblers, which are found naturally in montane scrub. Mountain parklike areas with scattered ponderosa pines are the only areas where Acorn Woodpeckers have been found and where Lewis' Woodpeckers breed in the study area. These species may have been present before the clearings were made but have certainly increased since. These parklike areas are also readily hunted by Red-tailed Hawks, which are infrequent in the neighboring dense woodland. The Rock Wren, surprisingly, is frequently observed in cleared woodland areas where dead trees are left scattered. The physiognomy of chained areas must bear enough resemblance to the open talus slopes this wren inhabits to allow it to occasionally utilize them. The Rock Wren has not, however, been found nesting in cleared woodland on Black Mesa. Ridgway observed this species in timber slash piles in California and Nevada in the late 1800s (in Ryser 1985). Sedgwick and Ryder (1987) report Rock Wrens breeding in chained woodland in Colorado.

Sedgwick and Ryder (1987) quantified the impacts on birds caused by chaining pinyon-juniper woodland in northwestern Colorado. Their results support my qualitative evaluation discussed above and can probably be applied to Black Mesa. Their study revealed that chaining caused an alteration in bird species composition and declines in overall bird use, density, species richness, and species diversity. They noted that species which were cavity or foliage nesters, foliage and bark gleaners, and aerial feeders underwent declines on a chained woodland plot. Specific species that declined in abundance due to chaining included the Hairy Woodpecker, Gray Flycatcher, Mountain Chickadee, Plain Titmouse, White-breasted Nuthatch, Solitary Vireo, and Black-throated Gray Warbler. The Mountain Bluebirds and Chipping Sparrows that utilized the chained plot accounted "for 48 percent of the avifauna." They found the Rock Wren breeding on the chained plot and said it was a "common" breeder even in chainings larger than 500 ha (1236 ac). In addition, species that "foraged and/or nested on the ground were less affected by the chaining process" than other groups.

Surface Mining Activities

Extensive deposits of subsurface coal made northern Black Mesa attractive for coal extraction. The opening of the first road over the northern rim of the mesa was associated with development of small underground mines (Johnston 1932). Peabody Coal Company began actual surface mining operations on its 25,900-ha (64,000-ac) lease in 1971 after several years of legal negotiations and preparation. Currently, about 243 ha (600 ac) is mined annually.

Reclamation practices, like woodland elimination, function ecologically as a habitat type conversion. Areas where native woodlands and shrublands stood before mining are planted to grasslands. This grassland-dominated range is developed to meet the primary designated postmining land use of livestock raising. Areas reclaimed as such are structurally simple, homogeneous communities and therefore do not support avifaunas as rich as the neighboring woodlands and shrublands. Such drastic geological (Hall 1983) and ecological changes in any surface-mined tract will markedly alter faunal assemblages found in them.

Pinyon-juniper woodland, sagebrush shrubland, and saltbush shrubland are the primary vegetation communities affected by mining. Leasewide, the areas mined or to be mined are covered by about 65% pinyon-juniper woodland, 30% sagebrush shrubland, and 5% saltbush shrubland. The total area reclaimed to grassland and grass-shrubland will be somewhat less than the total overall disturbance acreage since some roads, ponds, and facilities will be retained after mining. At the end of mining in about 2011, approximately 9771 ha (24,144 ac) will have been disturbed, of which about 8931 ha (22,069 ac) will be reclaimed. The total area of each habitat disturbed will be about 6238 ha (15,414 ac) of pinyon-juniper woodland, 3241 ha (8009 ac) of sagebrush shrubland, and 292 ha (721 ac) of saltbush shrubland. Until 1986, about 4295 ha (10,613 ac) had been disturbed.

Bird species richness and density generally decrease from native habitats to reclaimed areas. However, where shrubs are reestablished to sufficient densities at about 2720/ha (1100/ac) or higher, breeding bird richness and density may approach that of the shrubland habitats, particularly the mixed shrubland (see Tables 1–7).

Several studies have dealt with avian communities on reclaimed mine spoil. Apparently, few dealing with western sites have been published. Wray et al. (1982) found that sparrow productivity on a reclaimed site in West Virginia was insufficient to maintain their populations. Karr (1968) reported that the presence of water and diverse topography (in the form of ungraded spoil banks) greatly increased avian diversity on an abandoned mine site in Illinois. Krementz and Sauer (1982) compared a reclaimed site to an undisturbed desert scrub site in Wyoming and found that bird diversity was lower on the reclaimed site. In all, 12 species in 6 foraging guilds used the reclaimed site, while 37 species in 11 guilds occurred on the native site. Ground-gleaning guilds were predominant on the former. Horned Larks dominated the reclaimed site and were the only species breeding in it. Their reclaimed area was dominated by halogeton (*Halogeton glomeratus*), a weedy annual. Differences in avian communities on their sites were attributed to habitat structure. Hickey and Mikol (1979) surveyed breeding birds on mine spoil in Montana and Wyoming and compared them to native grasslands and shrublands. Their reclaimed area bird densities were lower than native sites with one exception and supported 4.2 species per site as compared to 4.0 and 8.0 species per site in grassland and sagebrush, respectively.

A major change associated with mining activities on northern Black Mesa is the construction of numerous (over 150 currently) water impoundment and sedimentation structures. Virtually all observations of shorebirds and waterfowl in the study area are a result of these man-made water impoundments. Red-winged Blackbirds nest only at these ponds. Only a few observations of Great Blue Heron, Black-crowned Night-heron, Mallard, Cinnamon Teal, Killdeer, Solitary Sandpiper, and Common Snipe have been recorded away from the ponds in perennial reaches of Coal Mine and Moenkopi washes. The largest impoundment, created in 1973, is J-7 pond on Red Peak Valley Wash. Two other large dams are located in Reed Valley and in Wild Ram Valley. Very few impoundments are over 15 years old. Thus, only recently have waterfowl and shorebirds become frequent visitors on northern Black Mesa, although in numbers much lower than at ponds in the neighboring Klethla, Kayenta, and Chinle valleys (personal observation).

The Common Raven, European Starling, and House Sparrow have all increased on northern Black Mesa as a result of surface mining activities. The raven exploits garbage and may feed extensively on seed heads of grasses in reclaimed areas. The latter two species are present at mine shops and other support facilities.

THE FUTURE

As the previous discussion noted, both the status and distribution of birds on Black Mesa are constantly changing. The last two decades were a period of unprecedented changes, the most pronounced of which were associated with habitat alterations resulting from mining and type conversions. The increase in waterfowl and shorebirds utilizing the lease as a result of pond construction, while not great compared to major wetlands, may be greater than at any time in the past several thousand years. Common Ravens are certainly more abundant now than ever before. Starlings and House Sparrows, most likely arriving in numbers only since 1970, have joined the Brown-headed Cowbird as recent emigrants. The Great-tailed Grackle may join these as well. For unknown reasons, the Cliff Swallow has apparently been recently lost as a breeding species. The chaining of nearly 3600 ha (10,000 ac) and mining and reclaiming of several thousand more hectares of woodland have allowed open-country species to increase and woodland species to be locally eliminated.

Tamarisk, whether one likes it or not, continues to spread and is now the single most important riparian vegetation type in the region. It is here to stay. Roads have penetrated farther into the upper canyons, and the clearing of pinyon-juniper woodland and sagebrush continues. Russian olive groves on lower Moenkopi Wash matured in a 7-year period to the point where a variety of wintering birds are now feeding on the abundant fruit and buntings were noted breeding in 1992.

These recent trends will continue. The rate of increase in the number of ponds will become slower and eventually stop. As mining comes to an end, the number will begin to decrease as ponds are reclaimed. Consequently, numbers of ducks and shorebirds will decline. The land reclaimed at the end of mining will form a complex of large grasslands. Open-country raptors such as Northern Harriers, Ferruginous Hawks, Rough-legged Hawks, and Merlins, as well as Northern Shrikes, will likely increase as migrants and/or winter residents, utilizing the reclaimed landscape. With the continued spread of tamarisk and Russian olive, some species such as Northern Orioles may begin breeding along the washes. Robins, Yellow-rumped Warblers, and White-crowned Sparrows will continue to increase as winter residents in these areas. The number of Killdeer breeding on the larger washes may decline if tamarisk continues to choke main channel beds. As grazing pressure mounts in the upper canyons, the understory of aspen groves and mixed-conifer woodlands will degrade further, with possible declines in scrub- and ground-dwelling species (e.g., MacGillivray's Warbler). Many species such as the Northern Goshawk, Spotted Owl, and other owls may be adversely affected if the last large, remote tracts of pinyon-juniper interspersed among the canyons of upper Coal Mine Wash are cleared. Many other changes to the bird life on Black Mesa will occur. Although the majority of species in the study area will exist in perpetuity (with some declining and others increasing), the likely trend, as human environmental pressures rise, is a decline in overall abundance and diversity and the loss of some species as breeding residents. I hope this report will help serve as a benchmark from which to gauge these coming changes both on Black Mesa and in the region as a whole.

SPECIES ACCOUNTS

The 241 bird species identified from northern Black Mesa are treated individually in this section. Six species are known only from archaeological remains. Ninety-seven species are confirmed as breeding in the area. An additional 12 are suspected breeders, 10 of which almost certainly do nest in the area. Forty-two families in 17 orders are represented. Status, period of occurrence, and habitat preferences are discussed. Subspecies designations are from Monson and Phillips (1981) and Behle (1985). Where these authors are in agreement, no citation is given. Where there is disagreement, differences are noted. Ranges of densities presented for smaller forms were extracted from the series of Peabody reports listed in the Literature Cited section.

Order Gaviiformes

FAMILY GAVIIDAE

Common Loon (*Gavia immer*). A fairly common migrant that has been observed only at J-7 pond. Most observations have been of single birds in alternate plumage from early April to early May. A single basic-plumaged bird was present at J-7 pond 8 June–5 October 1984. Four were seen on 3 April 1986 and 12 on 14 April 1987. Fall records include one on 6, 9, and 12 November 1986 and one on 30 October 1987.

Order Podicipediformes

FAMILY PODICIPEDIDAE

Pied-billed Grebe (*Podilymbus podiceps*). A common migrant at J-7 pond and other larger impoundments. Spring migrants appear in mid-March and are mostly gone by mid-May. It is common during the fall and into early winter until the ponds freeze. An adult with two young was observed on 18 June 1990 at Pond N14-F.

Horned Grebe (*Podiceps auritus*). A sparse migrant. One was observed on 4 April 1982, another on 13 December 1982, both at J-7 pond.

Eared Grebe (*Podiceps nigricollis*). A common to abundant migrant at J-7 pond. Spring migrants appear from mid-March to late May with numbers peaking in mid-April. Small numbers have been seen in late summer. Fall birds appear in mid-September and have been recorded until mid-December.

Western Grebe (*Aechmophorus occidentalis*). A fairly common migrant observed only at J-7 pond. Spring migration records are from April only. Fall migration is from July to November and peaks in October. No Clark's Grebes (*A. clarkii*) have been observed.

Order Pelecaniformes

FAMILY PELECANIDAE

American White Pelican (*Pelecanus erythrorhynchos*). A sparse migrant. Four individuals were observed at a pond in J-3 reclaimed area on 18 October 1984. Flocks observed at J-7 pond include 30 on 15 April 1986 (by B. Moreo), 1 on 8 October 1986, 215 on 13 October 1986, 27 on 5 October 1989, and 7 on 6 August 1990.

FAMILY PHALACROCORACIDAE

Double-crested Cormorant (*Phalacrocorax auritus*). A sparse transient. An immature individual was observed at a freshwater storage pond 17–24 August 1990.

Order Ciconiiformes

FAMILY ARDEIDAE

Great Blue Heron (*Ardea herodias*). A common migrant at J-7 pond and other impoundments throughout the lease. Rarely observed along the major washes. Spring migrants are seen from mid-March through May. Fall birds begin appearing in early July and are seen until the ponds freeze in December. One wintered at the old Kayenta Mine freshwater pond in 1984–85.

Great Egret (*Casmerodius albus*). A sparse transient. One was seen at J-7 pond 25 September–1 October 1990.

Snowy Egret (*Egretta thula*). A common migrant at J-7 and other ponds throughout the lease. Most are observed in April and May, August and September. Spring migrants have been seen until mid-June, and fall birds have been observed as early as late July.

Cattle Egret (*Bubulcus ibis*). A sparse migrant. One was reported by EH&A Consultants on 1 May 1980, one was seen at J-7 pond on 19 October 1984, three were seen at N-2 reclaimed area on 28 April 1988, two were at Pond CW-A on 22 August 1990, one was at N-1 reclaimed area on 23 April 1991, and three were at J-7 pond on 24 April 1992.

Black-crowned Night-heron (*Nycticorax nycticorax*). A fairly common migrant most often seen at J-7 pond, although an adult was seen in tamarisk on Moenkopi Wash 9 June and 27 August 1987. A dead immature in pre-basic molt was found on Coal Mine Wash at Navajo Rt 41 on 7 May 1985. Most records fall in May and from late August to mid-September. A lone immature was seen in N-2 reclaimed area on 24 July 1992.

FAMILY THRESKIORNITHIDAE

White-faced Ibis (*Plegadis chihi*). A common migrant at ponds throughout the area. Most are observed in April, May, August, and September (with smaller numbers noted in June and July) as singles and in small flocks. However, 60 were at J-7 pond on 29 August 1986, 183 were at N-1 reclaimed area on 3 May 1989, 100+ were seen soaring over N-1 reclaimed area on 16 April 1991, and 70 were at J-7 pond on 22 April 1992.

Order Anseriformes

FAMILY ANATIDAE

Snow Goose (*Chen caerulescens*). A sparse migrant. One was present at the reclamation barn on 17 and 18 November 1982, a second bird was seen in N-6 reclaimed area on 18 November 1982, and a "blue" morph individual was seen in N-14 reclaimed area on 24 February 1992 by C. Salt and S. Begay.

Ross' Goose (*Chen rossii*). A sparse transient. An adult was seen at Pond N14-D on 9 November 1989, and two were at J-7 pond on 10 April 1992.

Canada Goose (*Branta canadensis*). Primarily a fairly common migrant, but 15 wintered at J-7 pond in 1983–84. The largest group recorded was a northbound flock of 60 birds on 15 February 1991. Most records are from November and December. Small flocks have been seen feeding on wheatgrasses in reclaimed areas and resting on nearby ponds. Most birds seen are presumably *B. c. moffitti*, but a much smaller form(s) is frequently seen with the typical size birds.

Wood Duck (*Aix sponsa*). A sparse migrant. A female was seen at J-7 pond on 6 December 1985.

Green-winged Teal (*Anas crecca*). The most common migrant duck at ponds throughout the lease. Flocks of over 100 birds have been observed at J-7 pond. Most spring migrants pass through from mid-February to mid-April, but some are seen until mid-June. Males are most numerous early in this period and especially in late February and early March. Fall migration is primarily in August and September and is more drawn out than spring. A flock of nearly 100 birds was seen at J-7 pond on 6 December 1985 when males were in alternate plumage.

Mallard (*Anas platyrhynchos*). A common permanent resident at ponds throughout the lease. Spring numbers peak in mid-March. Twenty nestings at 12 ponds were noted from 1986 through 1992. Male Mallards were at the Coal Mine–Moenkopi Wash confluence on 20 December 1988 and 15 November 1989. The Mallard's occurrence on the leasehold increased during the 1980s, probably due to increasing numbers of sediment ponds.

Northern Pintail (*Anas acuta*). An uncommon migrant. An unsuccessful nesting occurred at N-1 reclaimed area in May and June 1985. Pintails are more numerous as basic-plumaged, late-summer and early fall migrants. In the spring they are quite sparse but most frequent during mid-March. On 11 October 1985, 15 alternate-plumaged males were seen at J-7 pond.

Blue-winged Teal (*Anas discors*). A fairly common spring migrant from mid-March to early May. Its fall status is unknown but it may be more frequent then than in spring (Jacobs 1986). A pair of adults was seen in N-1 reclaimed area on 17 June 1992.

Cinnamon Teal (*Anas cyanoptera*). A common spring migrant from mid-February to early May. Numbers peak in mid-April. A common fall migrant from July to October. Five birds were seen on Moenkopi Wash on 10 April 1992. Occasionally, small numbers may summer, but breeding has not been documented.

Northern Shoveler (*Anas clypeata*). A common migrant throughout the lease lingering into December at J-7 pond. Spring numbers peak in mid-April. Eleven were at Reed Valley Dam on 1 June 1988.

Gadwall (*Anas strepera*). A common migrant in small numbers at ponds throughout the lease. Seen from mid-February to early May and from late July to mid-December. Spring observations peak markedly in early April. On 19 June 1989, 13 were seen at Reed Valley Dam. Two individuals wintered in 1990–91.

Eurasian Wigeon (*Anas penelope*). Possibly a sparse migrant. Alternate-plumaged males in mixed *Anas* sp. flocks have been seen at J-7 pond (5 March 1982 and 17 March 1992), Reed Valley Dam (19 October 1988), and at ponds in the N-1 and N-2 reclaimed areas (10–27 November 1988). Another male, possibly the same individual seen November 1988, was observed at several ponds leasewide 20 October–5 December 1989.

American Wigeon (*Anas americana*). A fairly common spring and fall migrant, generally in small numbers, throughout the lease. Most fall occurrences are from late October to early December. Two individuals wintered in 1990–91.

Canvasback (*Aythya valisineria*). An uncommon migrant as singles or pairs at J-7 pond and at the old Kayenta Mine freshwater pond. It has been observed from October through April (no February records). One male was seen 5 August 1984.

Redhead (*Aythya americana*). A common migrant at J-7 and other larger ponds. Most birds pass through in March and April. Infrequent in the fall when most are seen in November. Single males were seen on 26 June 1986 and 6 July 1987.

Ring-necked Duck (*Aythya collaris*). A common migrant in small numbers seen most frequently at J-7 pond. Most records are from mid-March to early May. Notable concentrations include 60 at J-7 pond on 2 December 1987, up to 40 that wintered in 1989–90, and 60 that wintered in 1990–91.

Greater Scaup (*Aythya marila*). A sparse migrant. A pair was seen at J-7 pond on 2 April 1982.

Lesser Scaup (*Aythya affinis*). A common migrant seen most frequently at J-7 pond. This is the most numerous of the diving ducks found on the lease. Most spring migrants pass through from early March to early May. It is less numerous in the fall when most records are from October and November.

White-winged Scoter (*Melanitta fusca*). A sparse fall transient. A female was seen at J-7 pond on 30 October 1989.

Common Goldeneye (*Bucephala clangula*). A sparse spring migrant recorded primarily during March. There are five records: two females on 1 March 1984, three males and two females on 19 March 1984, single females on 8 and 20 March 1989, and a female seen at a pond in N-2 reclaimed area 4 March–4 April 1991.

Bufflehead (*Bucephala albeola*). A fairly common spring and fall migrant. Seen uncommonly through winter. Most birds pass through as singles or in groups of two to six individuals from March to mid-April. Most fall records are from late October and early November.

Hooded Merganser (*Mergus cucullatus*). A sparse migrant and winter resident. A male was seen on 17 November 1982 and a female on 3 November 1986, both at J-7 pond. On 20 March 1989, one male and three females were at J-7 pond. A female wintered at a freshwater storage pond December 1989–February 1990. Another female was at J-7 pond on 7 November 1990.

Common Merganser (*Mergus merganser*). A fairly common spring migrant at J-7 pond from mid-February to late April. Fall records include four females on 15 November 1982, seven females on 3 November 1986, and a single female 28 November–1 December 1988. Lone females were at Reed Valley pond on 19 June 1989 and J-7 pond on 9 June 1993.

Red-breasted Merganser (*Mergus serrator*). An uncommon spring migrant at J-7 pond with nearly all records from April. Seen twice in fall: a single female at J-7 pond on 17 November 1986 and six females there on 29 October 1987.

Ruddy Duck (*Oxyura jamaicensis*). A fairly common to common spring migrant from February to early May. It is less numerous in the fall and early winter. Most observations consist of five or fewer individuals. Seen occasionally at J-7 pond during the summer.

Order Falconiformes

FAMILY CATHARTIDAE

Turkey Vulture (*Cathartes aura*). A common summer resident seen throughout the area. However, numbers seem to have declined during the 1980s. This species appears regularly in the first week of April (the earliest being 23 March 1993), and the last are seen in early October. The latest was one seen on Dinnebito Wash on 8 October 1982. Breeding is unconfirmed, but this species probably uses numerous caves in the upper canyons as nest sites. An Anasazi granary in Moenkopi Wash appears to have been used as a nest site prior to 1987. In early July 1985 evidence was found of a small roost in an aspen grove in Coal Mine Wash. This roost was in use in late May 1986. Although occasionally seen feeding on small road-killed animals, most feeding observed has been on dead livestock, which is probably the primary food source of Turkey Vultures throughout the region. The breeding form in northeastern Arizona is not well known (see Monson and Phillips 1981).

FAMILY ACCIPITRIDAE

Osprey (*Pandion haliaetus*). A fairly common migrant observed widely throughout the area.

About half of all records are from J-7 pond where they have been observed feeding on green sunfish (*Lepomis cyanellus*) and largemouth bass (*Micropterus salmoides*). Seen three times on the mesa rim: Kayenta Point on 2 May 1985, Lolomai Point on 15 April 1987 and 1 April 1989. Most spring records are from April, with extreme dates of 25 March (1993) and 18 May (1988). Most fall occurrences are from September, but records range from 9 August (1990) to 15 October (1992).

Bald Eagle (***Haliaeetus leucocephalus***). A sparse early winter transient. A single adult was observed in Coal Mine Wash on 16 December 1982, an immature bird was seen over lower Yellow Water Canyon on 4 December 1984, and an immature was seen over Lower Moenkopi Wash on 20 December 1988. B. Moreo saw two adults at J-7 pond in January of 1985. One was seen over Dinnebito Wash on 16 March 1993. Leonard (1989) reports *Aquila/Haliaeetus* remains from Anasazi sites excavated on the lease (Table 13).

Northern Harrier (***Circus cyaneus***). A fairly common migrant and uncommon winter resident in open grasslands and shrublands throughout the area. Records range from 15 August (1991) to 1 May (1990). On 6 January 1982 one was observed feeding on a junco in the J-16 Mine Plan area.

Sharp-shinned Hawk (***Accipiter striatus***). A fairly common permanent resident. As a breeding bird it is found in mixed-conifer and aspen-oak habitats in the upper canyons (seven of nine nests). Ellis (personal communication) found a nest in pinyon-juniper woodland in 1982. This nest held three eggs on 4 June and two young ready to fledge on 23 July. Two active nests were found in late May 1986: one in a Gambel oak fringing an aspen grove and one with three eggs on 26 May in Rocky Mountain juniper in dense mixed-conifer. Three other vocal birds were found in early June 1986. It may be observed anywhere throughout the rest of the year as a migrant, but particularly in September and April. Late-spring migrants have been seen to mid-May. Bluebirds (*Sialia* sp.) accounted for 37% of the prey remains found below two perch sites in 1985 and 1986. Eight other prey species were identified from these remains. The breeding form is *A. s. velox*.

Cooper's Hawk (***Accipiter cooperi***). A fairly common to common permanent resident throughout the area, but quite sparse in winter. Migrant individuals may be seen anywhere. Breeding pairs are widespread and restricted to higher-elevation pinyon-juniper (where junipers appear to be selected for nest sites) and mixed-conifer woodland where it is common but inconspicuous. Several winters have no records. The first spring migrants may appear as early as late January, and the latest pass through in early May. However, the majority arrive in mid-March and are frequently seen into April. Resident birds arrive during this period, with territorial individuals being noted from mid-April to mid-May. Aerial courtship displays have been seen from late April to June. Eggs are apparently laid in mid- to late May and hatch in mid- to late June. Fledging takes place in mid- to late July, and possibly into early August for late clutches. Fledglings are conspicuous in or near breeding sites in August. Migrants are common from late August through October. Remains are reported from Anasazi sites excavated on the lease (Table 14).

Northern Goshawk (***Accipiter gentilis***). A fairly common winter resident in wooded sites throughout the area. More numerous in the 1983–84 winter. Two nests were found in mixed-conifer woodland: one with two young on 5 July 1987 and another on 20 June 1989. Nested in dense pinyon-juniper woodland in White House Valley in 1993. The breeding form is *A. g. atricapillus*.

Swainson's Hawk (***Buteo swainsoni***). A sparse migrant with four records: one seen at J-7 pond on 16 April 1984, one over the mesa rim on 19 June 1985, an immature over N-2 reclaimed area on 30 October 1990, and one over Reed Valley on 23 September 1991.

Red-tailed Hawk (***Buteo jamaicensis***). A common permanent resident throughout the area. Cliffs are preferred for nest sites where they are available. However, pinyons are preferentially selected over junipers in cliffless areas of the pinyon-juniper woodland. Larger, taller trees such as ponderosa pine and Douglas fir that occur in mixed-conifer/pinyon-juniper woodland ecotone are selected for nest sites in areas where suitable cliffs are unavailable. An estimated 12–18 pairs nested in or near the lease from 1982 to 1984 and again in 1992. Perhaps 75 pairs may nest in the study area during peak prey years. Egg laying occurs from late March to early May and, in one exceptional case, early March. Cottontails (*Sylvilagus* sp.) are the principal prey species, comprising 63% of prey taken (based on nest remains and observed kills). A nearly complete lack of nesting attempts in 1985 and the simultaneous reduction in number of adults observed from 1985 through 1988 (particularly in winter) may be related to very low cottontail numbers preceding and during this period. All breeding attempts during this period apparently failed. Low prey densities may have forced an adult to feed repeatedly on carrion (a road-killed dog) 7–9 February 1987. A "Harlan's" form was observed in White House Valley on 31 March 1983. The majority of breeding birds are light morphs. Only two dark morphs have been observed as breeding birds. Dark birds are more frequently observed as migrants. Three adults were observed at a nest containing young in late June 1984, indicating a possible helper role for one of them (see Santana et al. 1986). Collecting of young by Native Americans accounts for some nesting mortality in the area. Remains have been identified from Anasazi sites in the lease (Table 14). *B. j. calurus* is the breeding form.

Ferruginous Hawk (***Buteo regalis***). An uncommon migrant. One was seen in upper Reed Valley on 30 March 1983. Single birds seen 27–29 September 1983 at Dugout Valley, J-3 reclaimed area, and over lower Coal Mine Wash may have been the same individual. One was seen over Coal Mine Wash on 19 April 1985. Immatures were seen at J-27 reclaimed area on 10 September 1987 and at N-1 reclaimed area on 12 September 1988. Only one summer record: an immature seen over Moenkopi Wash at Navajo Rt 41 on 2 August 1988. A dark morph adult was seen hunting over N-1/N-2 reclaimed areas several times from 23 October 1988 to 3 January 1989. An immature was seen at N-1 reclaimed area on 2 May 1989. Possibly more common previously.

Rough-legged Hawk (***Buteo lagopus***). Usually a sparse winter resident and spring transient. One was observed by C. Kling of Mariah, Inc. Consultants at N-1 reclaimed area on 4 December 1984. One was seen over N-1 reclaimed area on 30 March 1987. A male wintered at the N-1 and N-2 reclaimed areas in 1987–88. Perhaps as many as 12 different individuals, mostly immatures, wintered at the N-7/N-8, N-1, N-2, N-14, J-1/N-6, J-16, N-14, and J-21 reclaimed areas in 1988–89. The first birds were seen on 23 October and the last on 7 April 1989. During November one was observed feeding on small rodents disturbed and exposed by a bulldozer and reclamation seeding drill operating in N-7/N-8 reclaimed area.

Golden Eagle (***Aquila chrysaetos***). A sparse permanent resident. Informants report current collecting of this species in the region by Hopis. Probably reduced in numbers from former times due to considerable use for religious and other practices by Native Americans. However, reduction of prey populations related to overgrazing may also play a role in low eagle densities in the region (Kochert et al. 1988).

FAMILY FALCONIDAE

American Kestrel (***Falco sparverius***). A common summer resident throughout the area. The uncommon November to mid-March wintering population is composed almost exclusively of males. This species may be abundant during peak migration periods in early April and late September–early October. Nests have been found in cavities of junipers, Douglas firs, and ponderosa pines, and in holes in alluvial banks and cliffs. Eggs and downy young have been seen in mid-June. Fledglings have been seen from late June to early August with most seen in mid-July. During the fall migration, kestrels feed extensively on grasshoppers in reclaimed areas. Horned Larks and Dark-eyed Juncos appear to be important winter prey species. A female caught a Violet-green Swallow in flight over J-7 pond on 18 September 1985. Another adult female was seen feeding on a Horned Lark at N-1 reclaimed area on 2 August 1989. Other vertebrates known to have been taken include a fledgling Sage Sparrow, several Mexican voles (*Microtus mexicanus*), horned lizards (*Phrynosona douglassi*), and *Sceloporus* sp. lizards. *F. s. sparverius* is the breeding form.

Merlin (***Falco columbarius***). A fairly common winter resident in open habitats throughout the area. The 31 records to date (most of which are from reclaimed areas) span from 24 October (1984) to 26 April (1991). Horned Larks probably form a staple of the winter diet, and hunting flights directed at this abundant winter reclaimed-area species have occasionally been seen. Merlins have been observed feeding on Horned Larks near J-3 reclaimed area (7 January 1983) and J-16 reclaimed area (2 January 1989). Another was feeding on a *Spizella* sparrow at N-2 reclaimed area on 21 April 1988. Most birds appear to be *F. c. richardsoni.*

Peregrine Falcon (***Falco peregrinus***). A sparse transient on the leasehold. Two were seen hunting Horned Larks at N-1 reclaimed area on 20 June 1984. Another pursued two Baird's Sandpipers at N-2 on 3 August 1987. An immature female was seen chasing a Mourning Dove in Long House Valley on 17 September 1985. Ellis (1982) reports a substantial breeding population from throughout Arizona.

Prairie Falcon (***Falco mexicanus***). An uncommon migrant and winter resident. Reported from a single Anasazi site (Table 14) by Rea (n.d.). Sparse as a breeding species with only two nesting sites known from the study area.

Order Galliformes

FAMILY PHASIANIDAE

Chukar (***Alectoris chukar***). A sparse introduced species. Birds released at J-7 reclaimed area in the fall of 1982 (three seen 22 September) have apparently not survived. Chukars were heard and tracks were found in talus at the mesa foot south of Owl Spring Valley on 13, 19, 27 October 1985 and 3 May 1989. Three birds were seen at the same area on 5 September 1989. They are probably descendants of transplants made near Chilchinbito by F. Taber in 1958 (Ryan personal communication).

Wild Turkey (***Meleagris gallopavo***). Reports of introductions near the mesa rim in the 1981 mine permit application are apparently unsubstantiated. No recent evidence of their occurrence in the study area has been found. This is the most frequently reported bird from excavated Anasazi sites that date almost continuously from A.D. 100 to 1150 (Table 14), suggesting its previous occurrence in the area, probably in the mixed-conifer habitats near the rim. Hargrave (1970) and McKusick (1986) think that feral domesticated turkeys established populations in the southwestern United States.

Northern Bobwhite (***Colinus virginianus***). Known from a single 12th-century Anasazi site (Table 14). If not a misidentification, this may have been *C. v. ridgway* (Masked Bobwhite) perhaps brought in by prehistoric trading activities.

Scaled Quail (***Callipepla squamata***). Known from a single 12th-century Anasazi site (Table 14).

Gambel's Quail (***Callipepla gambelii***). Known from a single Anasazi site. A *Callipepla/Lophortyx* (*sic*) determination is also reported (Table 14).

Order Gruiformes

FAMILY RALLIDAE

American Coot (***Fulica americana***). Common to abundant migrant at J-7 pond and other larger ponds from mid-March to early May and from late September to November. Smaller numbers are present in summer. It has nested at J-7 pond and sporadically at several others. Infrequent in winter.

Sora (***Porzana carolina***). A sparse migrant with seven records from late July to late September: one seen in tamarisk at J-7 pond on 24 and 27 August 1986, an immature flushed from weeds at a pond in N-2 reclaimed area on 12 September 1988, single adults at a pond in N-2 reclaimed area and in tamarisk below J-7 pond on 12 September 1991, one heard at a pond in N-10 reclaimed area, one in N-1 reclaimed area on 30 September 1991, and another there on 24 July 1992.

FAMILY GRUIDAE

Sandhill Crane (***Grus canadensis***). Known from a single Anasazi site (Table 14).

Order Charadriiformes

FAMILY CHARADRIIDAE

Semipalmated Plover (***Charadrius semipalmatus***). A sparse spring migrant. Two were seen at J-7 pond on 9 May 1983. On 26 April 1984 five were seen at J-7 pond and 14 at a pond near the N-5 pit.

Killdeer (***Charadrius vociferus***). A common permanent resident. It winters in small numbers and may leave during cold periods. Migrant birds pass through from early March to late April and in late September. Breeds at ponds and along the lower washes where densities of 1/620 m of wash bed were recorded over perennial reaches of Coal Mine and Moenkopi washes in late May 1986. Small young have been seen from mid-May to mid-July. The breeding form is *C. v. vociferus*.

FAMILY RECURVIROSTRIDAE

Black-necked Stilt (***Himantopus mexicanus***). An uncommon migrant. Two were seen at J-7 pond on 15 April 1983, five were seen there on 6 May, and three more on 20 May 1983. On 27 June 1983 three were seen at a pond in the N-1 reclaimed area. A flock of 23 was seen at J-7 pond on 16 May 1986.

American Avocet (***Recurvirostra americana***). An uncommon migrant. Six of the 10 records are from April, two from August, and one each from September and May. Usually seen in groups of five or less, but 19 were seen on 9 April 1982 at J-3 reclaimed area by B. P. Dunfee. Has been seen only once since 1985.

FAMILY SCOLOPACIDAE

Greater Yellowlegs (***Tringa melanoleuca***). A fairly common migrant as singles or pairs at ponds throughout the lease from late March to mid-April. A flock of 18 was seen at Kelly Pond on 14 April 1983. Seen in fall from late June to late November.

Lesser Yellowlegs (***Tringa flavipes***). A common migrant more frequently seen than the preceding species. Most records are from late April and September, but it has been observed in the region in all months between these periods.

Solitary Sandpiper (***Tringa solitaria***). A fairly common migrant from early July to late September. Usually seen as single individuals at ponds throughout the area. Two were seen at the confluence of Moenkopi and Yucca Flat washes on 13 August 1990. Two spring records: 23 April 1982 (two seen) and one on 19 April 1985.

Willet (***Catoptrophorus semipalmatus***). A fairly common migrant from mid-April to early May, and from early July through September. The largest flock seen was 34 birds at J-7 pond on 24 April 1992.

Spotted Sandpiper (***Actitis macularia***). A common migrant at ponds from mid-April to early June and mid-July to early October. Twenty seen at J-7 pond on 3 May 1991 were the largest recorded group. This species may breed at J-7 pond.

Long-billed Curlew (***Numenius americanus***). A sparse migrant. A single bird was seen at a pond in N-1 reclaimed area on 27 August 1985. Three were seen on 26 April 1982. One was at N-14 reclaimed area on 22 May 1988 and one at N-1 reclaimed area on 27 June 1989.

Marbled Godwit (***Limosa fedoa***). A fairly common spring migrant. All observations are restricted to the brief period of 9 April (1982) to 27 April (1990).

Western Sandpiper (***Calidris mauri***). A common migrant at ponds throughout the area. Most are seen in late April and early May and from early July to September.

Least Sandpiper (***Calidris minutilla***). A common migrant at ponds in late April and early May and from early July to early September. This species is considerably more frequent and numerous than the preceding. Larger flocks are seen occasionally: 18 on 18 April 1982 and 55 on 27 April 1984.

Baird's Sandpiper (***Calidris bairdii***). A fairly common fall migrant in late August–mid-September at ponds throughout the area.

Pectoral Sandpiper (***Calidris melanotis***). A sparse migrant. There are five records: one at J-7 reclaimed area on 7 October 1983, one in N-1 reclaimed area on 12 September 1985, three in J-7 reclaimed area on 30 September 1986, one at J-7 pond on 16 August 1990, and one in J-3 reclaimed area on 2 October 1991.

Long-billed Dowitcher (***Limnodromus scolopaceus***). A fairly common migrant with most records in the spring. A large flock of 86 was seen near the N-5 pit on 25 April 1984. On 8 October 1985, 11 were seen at J-7 pond. One was seen on 17 July 1989 in N-1 reclaimed area.

Common Snipe (***Gallinago gallinago***). A fairly common migrant in brushy aquatic areas. This species has been seen three times along the major washes: one at Moenkopi Wash–Reed Valley confluence on 18 April 1982, one at the confluence of Coal Mine Wash and Wild Ram Valley on 1 February 1984, and one below J-7 pond on 8 March 1985. Spring records are from early February to late April. Fall birds pass through from mid-August to early November. One was seen on 16 December 1992.

Wilson's Phalarope (***Phalaropus tricolor***). A common spring migrant from late April to mid-May. This species is a common late-summer and early fall migrant at ponds throughout the region (Jacobs 1986), but only five individuals have been observed from the study area in this period.

Red-necked Phalarope (***Phalaropus lobatus***). An uncommon spring migrant with most seen at J-7 pond. Twelve were seen on 12 May 1982, one on 30 August 1982, seven on 20 May 1983, and seven on 7 May 1986. One was at a pond in J-7 reclaimed area on 21 September 1989, and one was in N-2 reclaimed area on 24 August 1992.

FAMILY LARIDAE

Franklin's Gull (***Larus pipixcan***). An uncommon spring migrant from late March to late May.

Bonaparte's Gull (***Larus philadelphia***). A fairly common spring migrant from late March to early May at J-7 pond. Three fall records: two at J-7 pond on 10 November 1983, one on 13 November 1986, and one at Reed Valley pond on 2 November 1989.

Ring-billed Gull (***Larus delawarensis***). Common spring migrant at ponds throughout the area from early March through mid-May. Adults are most numerous early in this period, and progressively younger birds appear as the season passes. Considerably less numerous and frequent in the fall; three at J-7 pond on 28 November 1988 were late. Seen as singles to flocks of 30 or more, although 107 were at J-7 pond on 28 March 1988. An early fall individual was in Long House Valley on 3 August 1989. An immature seen at J-7 pond on 20 June 1983 was probably a late-spring migrant.

California Gull (***Larus californicus***). An uncommon spring migrant with most records in March and April. Four fall records: one on 17 October 1983, two at J-7 pond on 25 October 1985, three at J-7 pond on 27 October 1986, one there on 29 October 1987. Usually seen as singles or pairs with flocks of Ring-billed Gulls, but seven were seen on 27 March 1984.

Herring Gull (***Larus argentatus***). A sparse migrant. One was seen at J-7 pond on 14 April 1982.

Common Tern (***Sterna hirundo***). A sparse migrant. An adult and an immature were at J-7 pond on 9 September 1988. Three were seen at J-7 pond on 4 October 1983, six on 28 March 1984, and one on 20 April 1984. Two adults and an immature were seen at Reed Valley (Pond J28-G) on 25 August 1989. Another was at Pond J16-A on 21 September 1990.

Forster's Tern (***Sterna forsteri***). A fairly common spring migrant at J-7 pond, with most records restricted to the brief period of 26–30 April, plus a single adult on 18 May 1992. Three fall records: one on 17 August 1983, one 9–12 September 1986, and a single immature at Reed Valley Dam on 9 September 1988.

Black Tern (***Chlidonias niger***). A sparse late-summer migrant with four records: two at J-7 pond on 13 August 1984, two different individuals at J-7 pond on 13–17 August 1990, and one at pond N10-A on 10 September 1991.

Order Columbiformes

FAMILY COLUMBIDAE

Rock Dove (***Columba livia***). A sparse transient. Remains were found on the mesa rim on 1 August 1983. Three sight records: one at the mesa rim 15 miles east of the study area on 1 September 1984, another feeding along Navajo Rt 41 and Hwy 160 on 5–9 September 1989, and another at the Coal Mine Wash crossing of Navajo Rt 41 on 15 March 1991. Rock Doves are present in Kayenta and may stray into the study area.

Band-tailed Pigeon (***Columba fasciata***). Probably a sparse transient. One seen on Lolomai Point on 22 June 1985. This species may increase in numbers as the oaks invading Lolomai Point and other chained areas further increase in density and stature.

Mourning Dove (***Zenaida macroura***). A common summer resident throughout the area. Winters sporadically in small numbers at lower elevations. It usually arrives in early April and, except for stragglers, is gone by late September. A nest with two eggs was found in J-7 reclaimed area on 9 May 1985. Feathers of a fledgling were found on Yellow Water Wash on 25 June 1982. A breeding density of 3.8 pairs/40 ha was found in pinyon-juniper at J-10 mine plan area. The breeding form is *Z. m. marginella.*

Order Cuculiformes

FAMILY CUCULIDAE

Greater Roadrunner (*Geococcyx californianus*). Probably a sparse permanent resident in brushy valleys throughout the region. Nearly all Black Mesa records fall from August to late December. One was reported by B. Hector from lower Yucca Flat Wash (no date). J. Gilbert saw one at Black Mesa Junction 19 December 1984. One was seen in tamarisk on Moenkopi Wash on 27 August 1986. B. Clutter reported one in Dugout Valley on 8 August 1988. M. Koffler reported one on Moenkopi Wash on 15 September 1988. Another was seen in pinyon-juniper woodland in the J-1 mine plan area on 29 November 1988. One was seen on Navajo Rt 41 at Coal Mine Wash on 3 August 1989. C. Salt reported one on Navajo Rt 41 at Moenkopi Wash on 30 August 1989. Another was found road-killed in Long House Valley on 26 October 1989. The only spring record is one seen on 11 March 1993. The preponderance of late-summer through early winter observations from the study area and other areas of Black Mesa (personal observation) suggests that rather long-distance, post-breeding dispersal from primary breeding areas may be occurring. The Little Colorado River (Phillips et al. 1964) and the lower reaches of the Tusayan washes (e.g., Moenkopi Wash) may be such breeding areas.

Order Strigiformes

FAMILY STRIGIDAE

Flammulated Owl (*Otus flammeolus*). An uncommon summer resident. One was seen in Upper Reed Valley on 16 October 1982. A nest with young was reported from Long House Valley on 16 June 1936 (Woodbury and Russell 1945). Calling birds have been heard in the east fork of Coal Mine Wash in a mixed-conifer/oak/aspen habitat on 18 May 1986, on Lolomai Point on 31 May 1988, and in upper Moenkopi Wash on 12 May 1992. Another was seen in a cavity in an oak in the west fork on 9 June 1986. The breeding form is apparently undescribed (see Monson and Phillips 1981).

Western Screech-Owl (*Otus kennicottii*). An uncommon permanent resident in pinyon juniper woodland. Encountered primarily as road-kills: in Long House Valley 3 January 1983, at the foot of the mesa 4 miles west of Kayenta on 3 March 1984 and 3 December 1984, a molting adult in the J-21 mine plan area on 9 September 1988, and an adult female on Navajo Rt 41 near Yellow Water Wash on 15 July 1992. Remains were found in mixed-conifer on Coal Mine Wash on 1 July 1983 and one was seen in dense pinyon-juniper in Coal Mine Wash on 23 October 1984. Both the J-21 bird and the Navajo Rt 41 bird contained arthropods: six Jerusalem crickets (*Stenopelmatus* sp.) in the first and a large centipede in the latter. The wing chords of these individuals were 171 mm for the J-21 bird (indicating a female) and 176 mm for the Navajo Rt 41 female, making both larger than average for birds reported from Arizona (Phillips et al. 1964) and larger than any known from Utah (Behle 1985). Reported from Anasazi sites as well as an *Otus* sp. determination (Table 14). The breeding form is *O. k. aikeni.*

Great Horned Owl (*Bubo virginianus*). A fairly common permanent resident throughout the area. Nests have been found in old Common Raven and Red-tailed Hawk nests in trees and on ledges and potholes in cliffs in pinyon-juniper woodland on Yucca Flat Wash, Dinnebito Wash, and Moenkopi Wash. Nests on cliffs have been found in mixed-conifer in Coal Mine Wash (middle fork) and in Yellow Water Canyon. Eggs were seen on 5 April 1983 (J. Ohlman personal communication); half-grown young have been seen on 1 and 2 May 1983. Two nests found in 1989 contained three young, each on 18 May. Black Mesa birds show marked color variation typical of the local race, *B. v. pallescens.* Wing chord and/or weights of seven individuals found road-killed over 10 years are as follows: male, 21 September 1984, 330 mm, 875 g; male, 25 June 1990, 356 mm, no weight; male, 25 July 1990, 359 mm, no weight; female, 24 August 1985, 380 mm, 1300 g; female, 23 January 1987, 390 mm, 1284 g; female, 29 June 1989, 378 mm, 1063 g; female, 11 October 1991, 380 mm, 1432 g. These measurements, especially those of females, indicate that Black Mesa birds (if the above individuals are not migrants) are larger than *B. v. pallescens* from nearby southern Utah (Behle 1985).

Northern Pygmy-Owl (*Glaucidium gnoma*). An uncommon permanent resident. An increase in observations in fall indicates a possible influx of migrants. Most records are from mixed-conifer habitats. One was heard in Coal Mine Wash on 19 June 1982; another was seen on 20 June 1989 in the east fork of Coal Mine Wash. Two birds were seen and heard calling in Yellow Water Canyon on 8 August 1987, and another was seen on 30 September 1987. Remains were found in Coal Mine Wash from a probable *Accipiter* kill on 12 May 1986. *G. g. pinicola* is the breeding form.

Burrowing Owl (*Speotyto cunicularia*). Known only from a single Anasazi site (Table 14). I have seen this species just northeast of the study area, so it may be a sparse transient through it.

Spotted Owl (***Strix occidentalis***). At least a fairly common summer resident in shady mixed-conifer canyons and ravines. There are no winter records, but it is probably a permanent resident (Ganey and Balda 1989). Molted feathers have been found virtually across the extent of suitable habitat in the study area. All five known nest sites are in caves in cliffs adjacent to mixed-conifer–filled canyon floors. Laying takes place from late March to early May. Woodrats (*Neotoma* sp.) are the principal prey species identified from pellets (Ganey 1992). *S. o. lucida* is the race on Black Mesa.

Long-eared Owl (***Asio otus***). Sparse in pinyon-juniper and mixed-conifer. The only records are of one seen 29 March 1982 in J-28 mine plan area, one seen in White House Valley on 19 April 1983, remains of an adult found in a Great Horned Owl nest on 2 May 1983, a molted rectrix found in N-2 reclaimed area on 2 August 1989, and a fledgling and adult observed on 22 June 1990 at an abandoned Cooper's Hawk nest in pinyon-juniper in White House Valley. A single bird was in mixed-conifer on 18 June 1993.

Northern Saw-whet Owl (***Aegolius acadicus***). Prior to 1993, known only from a single feather (identified by J. T. Marshall) found in mixed-conifer at the head of Yellow Water Canyon on 23 June 1985. Marshall (personal communication) says this species may move into an area for a few years, nest, and then disappear. In the spring and summer of 1993, 10 were found in mixed-conifer.

Order Caprimulgiformes

FAMILY CAPRIMULGIDAE

Common Nighthawk (***Chordeiles minor***). A common summer resident from early June to September throughout the area. A nest with two eggs was found by C. Salt and S. Begay on 15 June 1989. A nest with one egg was found in pinyon-juniper on 1 August 1983 in the J-10 mine plan area. Two downy young were found near J-7 pond on 10 July 1985. The subspecies *C. m. hesperis* and *C. m. henryi* are reported from the area (Woodbury and Russell 1945), with the latter breeding. One late record from Yellow Water Wash on 7 October 1986.

Common Poorwill (***Phalaenoptilus nuttallii***). An uncommon summer resident in pinyon-juniper. This species appears to be uncharacteristically sparse on northern Black Mesa compared with the southern region of the Hopi Reservation (personal observation). Most records come from the pinyon-juniper–covered benches on the outer mesa scarp and consist of the following: four to six heard calling northwest of Tees Spa Spring on 29 April 1985, two seen below Tees Spa Spring on 5 July 1987, three heard there on 7 July 1987, one heard near Black Mesa junction on 3 June 1991, and four heard below Rock Gap on 4 June 1991. The only records from the interior of the mesa are of one seen in middle Coal Mine Wash on 26 April 1983, one heard calling in mixed-conifer in Coal Mine Wash on 5 June 1986, two heard in upper Moenkopi Wash on 11 May 1992, and one flushed from tamarisk on lower Moenkopi Wash on 23 July 1992. The nominate race is the breeding form.

Order Apodiformes

FAMILY APODIDAE

White-throated Swift (***Aeronautes saxatalis***). An abundant migrant and summer resident throughout the area from late March through mid-October. This species breeds in cliffs along the mesa rim and in the upper canyons. A steady stream of migrants was observed for several hours on 29 August 1984 at the rim where Navajo Rt 41 crosses. Thousands of migrants were seen over the lease area 21–25 September 1988. *A. s. saxatalis* is the breeding form.

FAMILY TROCHILIDAE

Black-chinned Hummingbird (***Archilochus alexandri***). A common summer resident in pinyon-juniper, along the major washes, and in mixed-conifer from late April to September. A female was seen on a nest in a pinyon near the head of the middle fork of Coal Mine Wash on 19 June 1982. S. Hamilton found a nest on a greasewood root along an alluvial bank on Moenkopi Wash in August 1983.

Calliope Hummingbird (***Stellula calliope***). A sparse migrant. One was seen among a swarm of Rufous Hummingbirds at a stand of bee plant (*Cleome serrulata*) on Yellow Water Wash on 22 August 1989. An adult male was seen near the Yellow Water Wash crossing of Navajo Rt 41 on 16 July 1990. A small female hummingbird, which may have been this species, was seen in the east fork of Coal Mine Wash on 20 June 1989. This date suggests this species may breed on Black Mesa.

Broad-tailed Hummingbird (***Selasphorus platycercus***). A common migrant throughout the area and a common breeding resident in mixed-conifer. Records range from early April to mid-September, with the last northbound males noted to late May. Two females on nests with eggs were found in Douglas firs in Coal Mine Wash on 23 and 27 June 1983. A nest with young was found by M. Williams in a ponderosa pine on 17 June 1985 at Lolomai Point. Fall migrants appear in mid-July.

Rufous Hummingbird (***Selasphorus rufus***). A common late-summer migrant. Usually first seen in mid-July, but may show up as early as late June. This species is often abundant at stands of Indian paintbrush (*Castilleja linariaefolia*) and Rocky Mountain bee plant.

Order Coraciiformes

FAMILY ALCEDINIDAE

Belted Kingfisher (*Ceryle alcyon*). A fairly common migrant from mid-April to early May and from mid-August to early October. Most records are from J-7 pond.

Order Piciformes

FAMILY PICIDAE

Lewis' Woodpecker (*Melanerpes lewis*). A fairly common summer resident in chained woodland at Lolomai Point. Seen once in a chained area on Kayenta Point on 25 September 1984. Young being fed in a ponderosa pine snag on Lolomai Point were seen on 17 June 1983 and 25 June 1986. An uncommon migrant elsewhere: three in pinyon-juniper at Dinnebito Wash on 8 April 1987, one above Black Mesa junction on 18 September 1987, one in pinyon-juniper in White House Valley on 13 September 1988, and one foraging with Pinyon Jays near J-3 reclaimed area on 19 September 1988. One was seen in pinyon-juniper on 17 December 1992.

Acorn Woodpecker (*Melanerpes formicivorus*). Fairly common in chained woodland areas. Breeding is unconfirmed. There are no winter records. Seen most frequently in the Kayenta and Lolomai points chained areas. *M. f. aculeatus* is the form present in this area.

Red-naped Sapsucker (*Sphyrapicus nuchalis*). A common migrant in wooded areas, including tamarisk on the larger washes. All records are from April, September, and October, except for one on 6 December 1991 seen feeding on Russian olive fruit. Small numbers were noted in tamarisk in Moenkopi Wash during September–October 1986.

Williamson's Sapsucker (*Sphyrapicus thyroideus*). A fairly common migrant in mixed-conifer. Apparently resident in very small numbers. A female was seen in Coal Mine Wash on 23 February 1983 and another female in pinyon-juniper in White House Valley on 19 January 1984. One pair was seen in pinyon-juniper near Lolomai Point on 27 February 1986; another pair was seen feeding young in a Douglas fir snag in dense mixed-conifer in the east fork of Coal Mine Wash on 23 June 1983. A vocal male was seen in Yellow Water Canyon on 23 June 1985. One record from tamarisk: a female seen on Moenkopi Wash on 10 October 1991.

Downy Woodpecker (*Picoides pubescens*). A sparse permanent resident more frequent in fall and winter. Seen in oaks in Yellow Water Canyon on 4 March 1984, in tamarisk on Lower Moenkopi Wash on 6 January 1986, and in aspens on Lolomai Point on 14 October 1986. Another was in the Russian olive grove on Moenkopi Wash on 12 December 1989. A single bird, probably breeding, was seen in aspens in Coal Mine Wash on 26 May 1986.

Hairy Woodpecker (*Picoides villosus*). A common permanent resident in pinyon-juniper and mixed-conifer woodlands. Nests with young (all in the third week of June) have been found in ponderosas, pinyons, and aspens. Densities of 1.8–4.4 individuals/40 ha have been found using Emlen transects. Breeding densities of 1.9 and 3.8 pairs/40 ha were determined with spot-mapping. This species was not found breeding in a woodland stand of 150 trees/ha. Black Mesa birds may be intermediates between *P. v. orius*, the breeding form according to Monson and Phillips (1981), and *P. v. leucothorectis* from nearby Navajo Mountain (Behle 1985).

Northern Flicker (*Colaptes auratus*). A common permanent resident in pinyon-juniper and mixed-conifer. A nest with young was found in a Gambel oak on 15 June 1984 in Coal Mine Wash. A nest with young was found in an aspen on 22 June 1985 in Yellow Water Canyon. Also, nests were found in holes in alluvial banks on lower Coal Mine and Moenkopi washes, where a nest contained five eggs on 8 May 1987, two nests held small nestlings on 6 June 1990, and another had young ready to fledge on 27 June 1990. Transect densities of 0.4–3.5 birds/40 ha have been observed. This species is frequent along the major washes in winter. Reported from a 12th-century Anasazi site (Table 14). The nomenclature of the breeding form from this region is presently under debate (see Monson and Phillips 1981 and Behle 1985).

Order Passeriformes

FAMILY TYRANNIDAE

Olive-sided Flycatcher (*Contopus borealis*). An uncommon fall migrant in August and late May–early June in pinyon-juniper and in mixed-conifer. One was found singing on the mesa rim on 17 June 1983.

Western Wood Pewee (*Contopus sordidulus*). A common migrant and sparse summer resident. Breeding in mixed-conifer is unconfirmed. Migrants are seen in pinyon-juniper and in tamarisk. A transect density of 8.6 birds/40 ha was found on Moenkopi Wash in mid-September 1985. Two were seen in tamarisk at the Reed Valley–Moenkopi Wash confluence on 10 June 1986. This species seems uncharacteristically sparse as a breeding bird considering the available habitat.

Willow Flycatcher (*Empidonax traillii*). A sparse migrant in riparian areas. Two were seen at the confluence of Moenkopi and Yucca Flat washes on 13 August 1990, another was there on 11 September 1989, one was seen at J-7 pond on 6 September 1989, and one was seen on lower Moenkopi on 13 August 1992. Seemingly more common as a transient in the larger lower valley areas throughout the region (Jacobs 1986, personal observation).

Hammond's Flycatcher (***Empidonax hammondii***). A sparse migrant. One was seen in tamarisk on Moenkopi Wash on 7 October 1986 and another was seen 7 May 1987. Perhaps more common than noted.

Dusky Flycatcher (***Empidonax oberholseri***). A common summer resident in open mixed-conifer associations with deciduous scrub understory. Nest building was observed on 30 May 1990. A nest with four eggs was found on 17 June 1985 in a thicket of *Prunus* below aspens in Yellow Water Canyon. Another nest with three young was found in an oak-covered slope in the same canyon on 23 June 1985, and young were being fed in a nest in a Douglas fir on 28 June 1992. Singing males have been seen on 30 April. Birds were seen in breeding habitat as well as in tamarisk on Moenkopi Wash in late August 1986.

Gray Flycatcher (***Empidonax wrightii***). A common summer resident in all but the lowest pinyon-juniper from mid-April to September. A nest with young was found in a juniper in White House Valley by B. Ebbers on 22 June 1983. Woodbury and Russell (1945) report two nests also in junipers. Adults with full-sized young have been seen from mid-June to mid-July. Transect densities range from 1.8 to 19.0 individuals/40 ha. Spot-map densities of 6.7–11.5 pairs/40 ha have been noted. Seen as late as 24 September (1986).

Cordilleran Flycatcher (***Empidonax occidentalis***). A common summer resident in mixed-conifer with deciduous scrub understory. This species is less numerous than the Dusky Flycatcher and occupies more shaded areas containing cliffs and banks for nesting. Nests with eggs were found on ledges in Coal Mine Wash on 24 June 1983 and 1 July 1985. Another with four eggs was found on 15 June 1986. Five short-tailed young were seen in Coal Mine Wash on 5 August 1985. *E. o. hellmayri* is the breeding form.

Black Phoebe (***Sayornis nigricans***). A sparse transient. One was seen on Moenkopi Wash near the confluence with Yucca Flat Wash on 29 June 1990.

Say's Phoebe (***Sayornis saya***). A common migrant and summer resident from late February to early November; one late bird seen on 6 December 1991. This species is distributed along larger open wash courses, rock outcrops, and near houses. Nests with eggs have been found as early as 20 April (1989). Nests with large young have been found on 28 May 1992 and 11 and 14 June (1985 and 1984, respectively). Fledglings have been seen on 29 June. Transect densities range from 0.3 to 24.0 individuals/40 ha. Summer densities are lower than spring, indicating a rather heavy influx of migrants. One was seen on the mesa summit in chained pinyon-juniper on 9 August 1986. Another was seen over dense pinyon-juniper on the mesa rim on 6 September 1986. The nominate race is the breeding form.

Ash-throated Flycatcher (***Myiarchus cinerascens***). A common summer resident in pinyon-juniper woodland throughout the area (absent from the highest, densest stands) but present in mixed-conifer habitats adjacent to shrub-filled canyon floors. Records range from 24 April to an abrupt mid-August departure. Spot-map densities of 3.8–7.6 pairs/40 ha have been recorded. Transect densities range from 0.6 to 12.4 individuals/40 ha. The nominate form breeds.

Cassin's Kingbird (***Tyrannus vociferans***). A common summer resident in open pinyon-juniper. Most numerous in the small canyons at the mesa foot. On 19 June 1986 nests with young were found on power poles at the Black Mesa Mine office and below Rock Gap. It has been seen by 27 April (1982); most leave by early September. Fledglings were seen at the mesa foot on 7 July 1985. *T. v. vociferans* is the breeding form.

Western Kingbird (***Tyrannus verticalis***). A fairly common migrant and a sparse summer resident. B. Ebbers found a nest near the Black Mesa Archaeological Project camp on 15 June 1983. Post-breeding dispersal from breeding habitats begins in mid-July, and migrants become common in early September.

Scissor-tailed Flycatcher (***Tyrannus forficatus***). A sparse transient. One was seen in juniper savanna in Long House Valley on 24 June 1993.

Eastern Kingbird (***Tyrannus tyrannus***). A sparse transient. One was seen at J-3 reclaimed area on 29 August 1988.

FAMILY ALAUDIDAE

Horned Lark (***Eremophila alpestris***). An abundant permanent resident in grasslands, open shrublands, and reclaimed areas. Flocks of up to 300 have been observed in reclaimed areas during midwinter when there may be an influx of northern birds. These winter flocks begin breaking up and males become territorial in late February. Nests with eggs have been found from mid-April to mid-May. Fledglings and new young have been found in late May. Mixed-age flocks begin forming by early July. Reported from a single early Anasazi site (Table 14). *E. a. occidentalis* is the breeding form.

FAMILY HIRUNDINIDAE

Purple Martin (***Progne subis***). A sparse migrant. A female was seen over Moenkopi Wash on 11 September 1986, and another was in N-1 reclaimed area on 24 August 1992.

Tree Swallow (***Tachycineta bicolor***). A common migrant near ponds from late March through May and from July to early October.

Violet-green Swallow (*Tachycineta thalassina*). A common migrant throughout the area. It is a common summer resident nesting in cliffs in the upper canyons and along the mesa rim and in holes in dirt banks along washes in areas of pinyon-juniper. Seen from 23 March (1990) to late September. *T. t. lepida* is the breeding form.

Northern Rough-winged Swallow (*Stelgidopteryx serripennis*). A common summer resident and migrant. This swallow breeds as widely scattered pairs in holes in alluvial banks along larger dissected wash courses. Records range from mid-April to mid-September. The form breeding in northeastern Arizona is not clear, but may be intermediate between *S. s. psammochrous* and *S. s. serripennis* (see Behle 1985 and Monson and Phillips 1981).

Bank Swallow (*Riparia riparia*). A common migrant. Seen most frequently at J-7 pond in August and September.

Cliff Swallow (*Hirundo pyrrhonota*). A common migrant throughout the area. Seen from 8 April (1982) to 13 September (1982). Old nest site foundations were found on a cliff on lower Moenkopi Wash on 1 July 1986 and below J-7 pond in 1987, but no active colonies were found from 1979 to 1990. Five vocal birds were seen at the Moenkopi Wash site on 1 July 1986, and an active colony appeared there in 1993. This species was unusually numerous throughout the study area in June 1989.

Barn Swallow (*Hirundo rustica*). A common migrant throughout the area from mid-April to early June and mid-July to mid-October. Breeding is known from a single nesting at the N-8 shop in 1992.

FAMILY CORVIDAE

Steller's Jay (*Cyanocitta stelleri*). A common permanent resident in mixed-conifer habitats. A few wander in the fall to lower areas of pinyon-juniper woodland, as at Owl Spring Valley on 13 October 1985. A nest with three young was found in Coal Mine Wash on 25 May 1986. Feathers of predated immatures were found on 27 May (1984) and on 4 July (1985). Family groups have been seen on 9 June (1984) and 16 June (1982). From Monson and Phillips (1981) and Behle (1985), it is unclear what the breeding form in this region is. It may be intermediate between *C. s. diademata* and *C. s. macrolopha.*

Scrub Jay (*Aphelocoma coerulescens*). A common permanent resident throughout the area in pinyon-juniper and mixed-conifer woodland, montane scrub, and tamarisk. Family groups in tamarisk on 8 June 1992 and 27 June 1990 indicate breeding. A nest containing four week-old young was found on 24 May 1990. Adults with fledglings have been seen from mid-May to late June. Transect densities in woodland range from 0.4 to 3.5 individuals/40 ha. Spot-map densities of 1.4–3.8 pairs/40 ha have been found in pinyon-juniper woodland. Remains are reported from a single Anasazi site (Table 14). Monson and Phillips (1981) call the birds in this region *A. c. suttoni.* Behle (1985) calls them *A. c. woodhousei.*

Pinyon Jay (*Gymnorhinus cyanocephalus*). A common permanent resident throughout the area. Adults building nests have been seen on 8 March (1982). Nests with young and/or eggs have been seen in early May. Young fledglings have been seen from 13 April to the surprisingly late date of 12 July (1982). Flocks of Pinyon Jays are occasionally seen feeding on wheatgrasses in reclaimed areas. During the fall Pinyon Jays form the largest bird flocks in the area. On 10 September 1983, 285 were seen at the mesa foot. On 23 September 1983, over 470 were seen at Reed Valley. A loose aggregation of several flocks totaling nearly 600 individuals was seen at Dinnebito Wash on 19 January 1984. Reported from three Anasazi sites (Table 14).

Clark's Nutcracker (*Nucifraga columbiana*). A fairly common to common permanent resident in the upper canyons. It occasionally wanders widely in late summer and fall to the pinyon-juniper below the mesa rim. Fledglings have been seen in the upper canyons from 24 May (1985) to 22 June (1983). Remains of a young fledgling were found in Moenkopi Wash on 13 April 1989. These dates indicate that laying takes place from early March to mid-May. A mixed-age flock of 35 individuals was seen in Coal Mine Wash on 30 May 1990. This species apparently left the mesa rim region during most of the 1985–86 winter.

American Crow (*Corvus brachyrhynchos*). A sparse migrant. One was seen near J-3 reclaimed area on 16 November 1987, two at the highway crossing of Coal Mine Wash on 28 March 1988, and one at N-14 on 13 November 1991. Another was seen on 6 November 1989. Known from a single Anasazi site (Table 14).

Common Raven (*Corvus corax*). An abundant permanent resident areawide. The population in the lease is probably artificially high because of readily available food in garbage, waste grain in straw mulch, and other sources. Adults frequenting nest sites and building nests have been seen on 15 January (1985). Nests with eggs have been found by early May. Young of all ages have been found from late May to early July, but most fledge by mid-June. Flocks of over 100 birds have been seen feeding on cured seed heads in reclaimed areas on several occasions. Approximately 100 birds were observed using Russian olives for a nocturnal roost on 23 January 1992. Remains are reported from Anasazi sites (Table 14).

FAMILY PARIDAE

Mountain Chickadee (***Parus gambeli***). A common permanent resident in higher-elevation pinyon-juniper and mixed-conifer throughout the area. Small numbers occupy tamarisk of the larger washes in fall and winter. Song activity is frequent by early March. Nests with young and eggs have been found during the first three weeks of June, and fledglings have been seen from mid-June to mid-July. Transect densities in pinyon-juniper range from 1.8 to 32.2 individuals/40 ha. Spot-map densities range from 3.8 to 11.5 pairs/40 ha. Monson and Phillips (1981) call birds in this region *P. g. wasatchensis*, but Behle (1985) would assign them to atypical *P. g. gambeli.*

Plain Titmouse (***Parus inornatus***). A common permanent resident in pinyon-juniper but generally absent in the highest-elevation stands. Fall transients have been seen twice in tamarisk. A nest with young ready to fledge was found on 13 June 1982. Family groups have been seen from mid-June to mid-July. Transect densities in pinyon-juniper range from 1.8 to 30.2 individuals/40 ha. Spot-map densities range from 7.6 to 11.5 pairs/40 ha. The breeding form is *P. i. ridgwayi.*

FAMILY AEGITHALIDAE

Bushtit (***Psaltriparus minimus***). A common permanent resident in pinyon-juniper and mixed-conifer throughout the area. A nest was found in tamarisk on Moenkopi Wash on 25 May 1993. Flocks wander into shrublands and tamarisk during fall and winter, begin to break up into pairs by late March, and are forming again by late June. B. Ebbers found an active nest in June 1983 that had fledged young by the 15th. Family groups were noted in 1992 on 29 May and 5 June. Pinyon-juniper transect densities range from 1.8 to 31.3 individuals/40 ha. Spot-map densities of 3.8–5.7 pairs/40 ha have been recorded. The breeding form is *P. m. plumbeus.*

FAMILY SITTIDAE

Red-breasted Nuthatch (***Sitta canadensis***). An irregularly common winter resident in mixed-conifer. A sparse summer resident in the same areas. An adult with an immature seen at Lolomai Point on 7 August 1990 may not represent local breeding. However, family groups seen on 28 July 1992 and 16 June 1993 confirm local nesting. Two were seen in pinyon-juniper in White House Valley on 10 August 1984. This species was common in the upper canyons in the 1984–85 winter when a heavy, widespread Douglas fir cone crop ripened. It was absent the following winter when no cones were produced.

White-breasted Nuthatch (***Sitta carolinensis***). A common permanent resident in pinyon-juniper woodland and in mixed-conifer. This species does not breed in lower-elevation pinyon-juniper where it was absent as a breeding species in a stand of 150 trees/ha. Spot-map breeding densities in pinyon-juniper range from 3.8 to 11.5 pairs/40 ha. Transect densities range from 1.4 to 14.8 individuals/40 ha. Nests with young have been found from late May to mid-June. Family groups have been seen from mid-June to mid-July. The breeding form is *S. c. nelsoni.*

Pygmy Nuthatch (***Sitta pygmaea***). A common permanent resident in flocks in ponderosa pine–dominated mixed-conifer association. Strays to adjacent pinyon-juniper in late summer and fall. Fledglings have been seen from mid-June to late July. The breeding form is *S. p. melanotis.*

FAMILY CERTHIIDAE

Brown Creeper (***Certhia americana***). A fairly common permanent resident in mixed-conifer. Seen once in pinyon-juniper in winter: 5 January 1983 in White House Valley. Young were seen being fed in a nest on a Douglas fir in Yellow Water Canyon on 22 June 1985, and a family group was seen in Coal Mine Wash on 2 July 1992. The breeding form is *C. a. montana.*

FAMILY TROGLODYTIDAE

Rock Wren (***Salpinctes obsoletus***). A common summer resident of talus slopes, rock outcrops, alluvial banks, and riprap of dam spillways and road slopes. Birds are present on the lease from early March to early December, but numbers decrease sharply in early October. One midwinter record was 20 January 1992. Numerous family groups were noted 11–12 June 1992. On 20 June 1983 a nest with six eggs was found at Tees Yah Toh Spring. On 19 July 1984 a family group was seen below J-7 dam. It is frequently seen in chained pinyon-juniper on the mesa summit. The nominate race breeds.

Canyon Wren (***Catherpes mexicanus***). A common permanent resident in the cliffs of the upper canyons, along the Dakota Sandstone, and in other cliff and talus areas. During fall and winter it is seen along alluvial banks and occasionally at small rock outcrops. Family groups have been seen from mid-June to early July. A nest with a fledgling was found on 27 July 1987. *C. m. consperus* is the breeding form.

Bewick's Wren (***Thyromanes bewickii***). A common summer resident in pinyon-juniper and mixed-conifer. Fairly common in winter when it wanders into shrublands and tamarisk. Males are actively singing by late February. Nests, both in junipers, with eggs were found on 2 and 11 June 1982. Family groups have been seen by 20 June and 2 July. Transect densities in pinyon-juniper range from 1.8 to 28.8 individuals/40 ha. Densities of 11.5–32.5 individuals/40 ha have been recorded in shrubland areas in late summer. Spot-map breeding densities range from 11.5 to 19.1 pairs/40 ha in pinyon-juniper. Uncommon as a breeding bird in the densest pinyon-juniper on the mesa summit. The breeding form is *T. b. oberholser.*

House Wren (***Troglodytes aedon***). A common migrant along washes in tamarisk. A common summer resident in aspen groves. Migrants are usually seen in spring in late April and early May, but one on 11 April 1989 was atypically early. Most fall migrants pass through from late August to mid-October, with one on 31 October 1989 being late. A nest with young in an aspen was found on 15 June 1984. Young fledglings were seen in the east fork of Coal Mine Wash on 24 June 1984. Several individuals were observed in slash piles in the Kayenta Point chaining on 14 June 1986. Sedgwick and Ryder (1987) report this species in pinyon-juniper slash in Colorado. Post-breeding dispersal away from aspen groves into adjoining mixed-conifer woodland begins in mid- to late June. *T. a. parkmani* is the breeding form.

Winter Wren (***Troglodytes troglodytes***). A sparse migrant. One was seen in an aspen grove in the west fork of Coal Mine Wash on 6 November 1983. Another was seen in the same grove on 15 November 1986.

Marsh Wren (***Cistothorus palustris***). A fairly common migrant at weedy or brushy pond edges. One was seen by EH&A Consultants on 5 October 1979. Seen at a pond in N-2 reclaimed area and in tamarisk at J-7 pond several times in early September 1986. One was seen at Pond N14-G on 12 March 1989 and at N-2 reclaimed area on 12 and 28 April 1989.

FAMILY MUSCICAPIDAE

Golden-crowned Kinglet (***Regulus satrapa***). A fairly common fall, winter, and early spring resident in mixed-conifer of the upper canyons. Records range from 12 October (1988) to 4 March (1984).

Ruby-crowned Kinglet (***Regulus calendula***). A common migrant in wooded areas throughout the area. A fairly common summer resident in mixed-conifer in the upper canyons. Breeding is unconfirmed. One was seen in Russian olives on 9 December 1992. Singing males have been recorded throughout June in all of the upper canyons including five on 16 June 1982 in the middle fork of Coal Mine Wash. Transect densities of migrants range from 1.8 to 10.6 individuals/40 ha. Monson and Phillips (1981) call Arizona breeding birds *R. c. calendula*, but Behle would assign birds of this area to *R. c. cineraceus*.

Blue-gray Gnatcatcher (***Polioptila caerulea***). A common summer resident in higher-elevation pinyon-juniper and in areas of deciduous scrub. A nest with young near fledging was found in a pinyon near Tees Spa Spring on 5 July 1987. An old nest was found in a small pinyon in Reed Valley in December 1988. Wanders into sagebrush in late summer. Seen from mid-April to late October. Migrants are frequent in tamarisk. Transect densities range from 2.3 to 9.4 individuals/40 ha. All spot-map densities are 3.8 pairs/40 ha. The breeding form is *P. c. obscura*.

Western Bluebird (***Sialia mexicana***). A common permanent resident throughout the area. It breeds in higher-elevation pinyon-juniper and mixed-conifer woodland. Pinyon-juniper stands of 150 and 182 trees/ha contained no nesting individuals. It may be absent during periods of cold and deep snow in midwinter. Nests with young have been seen from mid-June to late July. Pinyon-juniper transect densities range from 1.8 to 8.9 individuals/40 ha. A spot-map density of 3.8 pairs/40 ha has been found. *S. m. occidentalis* is the breeding form.

Mountain Bluebird (***Sialia currucoides***). A common permanent resident of pinyon juniper throughout the area. It may be absent during extreme cold and heavy snow in midwinter but was seen several times in winter at the Russian olive grove on Moenkopi Wash. It consistently appears by late January and is common by late February. The largest flock recorded was 250 in the Russian olive grove on 29 January 1992. Mountain Bluebirds occupy more open areas such as sage clearings and chained pinyon-juniper. It frequently nests in holes in alluvial banks (nestlings being fed in such situations were seen 4 June 1991 and 12 May 1992) and cliffs (nest with eggs and young seen 28 May 1992). Nests with young have been seen in mid- and late June. Pinyon-juniper transect densities range from 0.9 to 16.0 individuals/40 ha. Spot-map densities range from 1.8 to 7.6 pairs/40 ha.

Townsend's Solitaire (***Myadestes townsendi***). A fairly common to common permanent resident in mixed-conifer of the upper canyons. It has been seen occasionally in pinyon-juniper elsewhere. Fledglings have been seen from early July to early August. An old nest was found in a hole in a boulder in Coal Mine Wash on 6 September 1986. *M. t. townsendi* is the breeding form.

Hermit Thrush (***Catharus guttatus***). A fairly common migrant throughout the area. A common summer resident in mixed-conifer of the upper canyons. Singing has been heard in late April. Stubby-tailed fledglings have been seen on 27 June (1983, 1985) in Coal Mine Wash and Yellow Water Canyon, respectively. The breeding form is *C. g. auduboni*. Occasionally heard singing in summer in dense pinyon-juniper as at White House Valley on 17 June 1983 and 20 June 1984.

American Robin (***Turdus migratorius***). A common migrant throughout the area and a fairly common summer resident in mixed-conifer of the upper canyons. Nested in pinyon-juniper in 1993 (adults with fledgling seen 26 June). Uncommon and irregularly seen in winter until about 1990 when up to 70 began wintering in Russian olives. An incubating adult was seen in oaks fringing an aspen grove in Yellow Water Canyon on 15 June 1986. Woodbury and Russell (1945) report breeding from Black Mesa. *T. m. propinquus* is the breeding form.

Varied Thrush (***Ixoreus naevius***). A sparse fall transient. One record: an adult male was seen with robins in Russian olives on Moenkopi Wash on 12 November 1992.

FAMILY MIMIDAE

Northern Mockingbird (***Mimus polyglottos***). A common summer resident in juniper savanna at the mesa foot and in greasewood and tamarisk on lower washes and in smaller drainages in mixed shrublands. One seen 14 March 1989 was exceptionally early by six weeks. Seen in oaks in the Lolomai Point chaining on 14 July 1984. A nest in greasewood contained four eggs on 6 June 1990. A fledgling was seen in juniper savanna on 3 July 1985. A transect density from Moenkopi Wash is 5.3 individuals/40 ha. The nominate race is the breeding form.

Sage Thrasher (***Oreoscoptes montanus***). A common summer resident in greasewood and saltbush in the middle to lower reaches of the major washes. It is less numerous in sagebrush. The first spring appearance is usually in early April. A nest in saltbush in a mixed-shrub habitat contained three young on 19 June 1986. Fledglings were seen in Reed Valley on 21 July 1982. Sage Thrashers are common in J-7 reclaimed area where saltbush is well developed (3.3 pairs/40 ha). Transect densities range from 0.9 to 9.5 pairs/40 ha.

Bendire's Thrasher (***Toxostoma bendirei***). A fairly common summer resident in open greasewood in lower washes and in juniper savanna at the mesa foot. Small numbers are found in open saltbush in mixed shrubland. Records span from mid-April to August. A nest with three small young was found in a juniper at the mesa foot on 18 June 1986. A transect density of 1.8 individuals/40 ha was recorded on Moenkopi Wash in 1980 by EH&A Consultants.

FAMILY MOTACILLIDAE

American Pipit (***Anthus rubescens***). A common migrant at ponds and reclaimed areas throughout the area. Sparse in winter at unfrozen ponds. Spring migrants peak in April and have been seen from mid-February to early May, with a single bird seen 3 June 1991 being late. Fall migrants are seen from mid-August to early December with peak numbers in October. Usually seen in small groups, but a flock of 41 was seen on 12 April 1989 in N-1 reclaimed area, and over 200 were seen there on 26 April 1991.

FAMILY BOMBYCILLIDAE

Bohemian Waxwing (***Bombycilla garrulus***). Two records: a flock of 29 was seen in pinyon-juniper in White House Valley on 13 April 1982 and a single bird in Russian olives on 12 November 1992.

Cedar Waxwing (***Bombycilla cedrorum***). A sparse fall migrant with records as follows: six seen in Dinnebito Wash on 16 November 1982, seven in mixed-conifer in Coal Mine Wash on 22 October 1983, one over Moenkopi Wash on 10 October 1986, two near "Kelly Pond" on 12 September 1991, one in Russian olives on 15 November 1990, and eight there on 29 January 1992.

FAMILY LANIIDAE

Northern Shrike (***Lanius excubitor***). An uncommon to fairly common winter resident in open pinyon-juniper from mid-October to late March. A large invasion occurred in 1988–89, with more birds seen during this period than in the previous seven winters combined.

Loggerhead Shrike (***Lanius ludovicianus***). A fairly common to common permanent resident in juniper savanna and greasewood in the major washes. Seen less frequently in other open shrubland. The 1984 spot-map density in mixed-shrub habitat was 0.8 pairs/40 ha. Fledglings and family groups have been noted from early June to early July. The breeding form is *L. l. excubitorides* (see Monson and Phillips 1981).

FAMILY STURNIDAE

European Starling (***Sturnus vulgaris***). A common permanent resident that is local in the study area. Starlings frequent the reclamation barn and the area near the mine facilities. This species was probably absent from the area prior to the mine development in the late 1960s. The largest group seen was a flock of 350 in Russian olives on Moenkopi Wash on 15 November 1990. This species appears to be widely dispersed throughout the region during winter.

FAMILY VIREONIDAE

Gray Vireo (***Vireo vicinior***). A fairly common summer resident from 23 April (1992) to 10 September (1983). Most observations are from open pinyon-juniper–covered slopes and small canyons that support a scattered growth of Utah serviceberry. A nest with two small young was found in a small pinyon above Tees Yah Toh Spring on 20 June 1986.

Solitary Vireo (***Vireo solitarius***). A common migrant and summer resident in pinyon-juniper woodland and in mixed-conifer of the upper canyons. Records span from 22 April (1983) to 7 October (1982). The migrant form, *V. s. cassinii*, has been seen in the fall. A nest with young was found on 21 June 1983 in lower Reed Valley and in White House Valley. An adult with a full-sized fledgling was seen in White House Valley on 27 July 1982. A flock of 10 was seen on the rim of Yellow Water Canyon on 11 May 1984. Transect densities range from 0.4 to 12.4 individuals/40 ha. Spot-map densities range from 1.9 to 7.6 pairs/40 ha. The breeding form is *V. s. plumbeus*.

Warbling Vireo (***Vireo gilvus***). A common summer resident of aspen groves in the upper canyons. A common migrant in tamarisk from early August to mid-October. The breeding form is *V. g. brewsteri*.

FAMILY EMBERIZIDAE

Tennessee Warbler (***Vermivora peregrina***). A sparse transient. A single bird was seen in tamarisk on Moenkopi Wash on 7 October 1986.

Orange-crowned Warbler (***Vermivora celata***). A common migrant in deciduous scrub and tamarisk throughout the area. Transect densities as high as 177 individuals/40 ha have been recorded in tamarisk (1 October 1986). A fairly common summer resident in mixed-conifer in the upper canyons. Breeding habitat is Gambel oak–covered slopes usually adjacent to aspen groves and with a grassy, leaf-littered understory. A pair of adults was found with fledglings in the west fork of Coal Mine Wash on 27 June 1983. Records span from 1 May (1983) to 22 October (1986). The breeding form is *V. c. orestera*.

Nashville Warbler (***Vermivora ruficapilla***). A common to abundant fall migrant in montane scrub and tamarisk from early August to early October.

Virginia's Warbler (***Vermivora virginiae***). A common to abundant migrant areawide. A common summer resident in montane scrub of the upper canyons, upper mesa slopes, and Lolomai Point chained area. Records span from mid-April to early October. Several pairs with young fleglings were found on 15 June 1986. Fall migrants appear in tamarisk along the lower washes beginning in late June and become progressively more common, peaking in late August. The breeding form is *V. v. virginiae*.

Lucy's Warbler (***Vermivora luciae***). A sparse transient: a singing male was seen in tamarisk on Moenkopi Wash (elevation 1768 m) on 11 April 1992.

Yellow Warbler (***Dendroica petechia***). A common fall migrant in tamarisk along the major washes from early August to early October. Apparently sparse in spring: one in aspens in Yellow Water Canyon on 5 May 1987, one in pinyon-juniper on 6 May 1987, one at J-28 settling ponds on 20 May 1990, and a singing male in Russian olives on 8 June 1992. A nonbreeding, singing male was seen in tamarisk on Moenkopi Wash on 26 June 1990. See Monson and Phillips (1981) concerning the complex of races migrating through the region.

Yellow-rumped Warbler (***Dendroica coronata***). A common to abundant migrant throughout the area. Up to 713 per 40 ha were recorded in tamarisk on Moenkopi Wash (26 September 1986). A fairly common summer resident in mixed-conifer of the upper canyons. Spring migration peaks in late April–early May, and fall migration peaks in late September–mid-October. (Records of migrants span from 13 April to 8 December.) By 1990 this species was wintering in small numbers in Russian olives on Moenkopi Wash. Two adults were seen feeding young in a ponderosa on 16 June 1984 on Kayenta Point. A fledgling was found on 14 June 1986. An adult male in pre-basic molt was seen in upper Moenkopi Wash on 30 July 1985. A male "myrtle" form was seen in J-27 reclaimed area on 27 April 1982. Monson and Phillips (1981) call the breeding form *D. c. memorablis*, but Behle (1985) assigns it to *D. c. auduboni*.

Black-throated Gray Warbler (***Dendroica nigrescens***). A common summer resident of pinyon-juniper and mixed-conifer woodland. Records span from 8 April (1991) to 21 September (1982). The males, initially seen in small groups, are singing and actively defending territories by late April. Females have been observed nest building from mid- to late May. A nest on 25 May contained four eggs. Young in nests have been found on 8 and 17 June. Fledglings have been seen 25 June–27 July. Adults were seen feeding young Brown-headed Cowbirds on 19 July and 4 August 1982. Transect densities range from 0.9 to 26.6 individuals/40 ha. Spot-map densities range from 7.6 to 15.3 pairs/40 ha. Monson and Phillips (1981) recognize the subspecific rank of *D. n. halsei* as the breeding form in the region. Breeding densities correlate positively with pinyon density, and this species appears to forage preferentially in pinyons. Further study may prove it to be a pinyon specialist in the Black Mesa area.

Townsend's Warbler (***Dendroica townsendi***). A common fall migrant in mixed-conifer of the upper canyons. Fairly common in aspens, pinyon-juniper, and tamarisk. Records range from 21 August (1992) to 22 October (1986).

Hermit Warbler (***Dendroica occidentalis***). A sparse fall migrant. An immature female was seen in tamarisk on Moenkopi Wash on 29 September 1989.

Grace's Warbler (***Dendroica graciae***). A common summer resident in ponderosa pine–dominated mixed-conifer woodland. Adults with fledglings were seen on 16 June and 13 July 1984 in the west fork of Coal Mine Wash. Woodbury and Russell (1945) report collecting two adults and an immature in July 1938. Records range from 18 April (1989) to 6 September (1986).

American Redstart (***Setophaga ruticilla***). Remains were found near the mesa rim by D. Ellis (personal communication) in 1983. Probably a sparse migrant.

Northern Waterthrush (***Seiurus noveboracensis***). A sparse migrant. One was seen at a pond in J-27 reclaimed area on 13 May 1982, one in tamarisk on Moenkopi Wash on 12 May 1987, and another in mixed-conifer on 7 May 1992. One was seen in tamarisk on 16 September 1992.

Kentucky Warbler (***Oporornis formosus***). A sparse transient. An adult male was seen in montane scrub at the head of the east fork of Coal Mine Wash on 7 May 1983. Another adult was seen in tamarisk on Moenkopi Wash on 17 September 1986.

MacGillivray's Warbler (***Oporornis tolmiei***). A common migrant in montane scrub and tamarisk. It is most numerous during fall migration, which peaks in late August to mid-September, but it is seen until mid-October. An uncommon breeding resident of montane scrub at three localities in the upper canyons. An adult male in Yellow Water Canyon was seen feeding a fledgling in a dense tangle of oaks, aspen, chokecherry, clematis, and dogwood on 23 June 1986. Six adults (three carrying food) were seen in a similar habitat on 20 June 1986 in the east fork of Coal Mine Wash. The breeding form is *O. t. monticola*. Grazing may threaten this species as a breeding bird on Black Mesa.

Common Yellowthroat (***Geothlypis trichas***). A fairly common migrant in early May and from late August to early October in tamarisk on Moenkopi Wash and at weedy ponds. A singing, nonbreeding adult male was seen on Moenkopi Wash on 27 June 1990.

Wilson's Warbler (***Wilsonia pusilla***). A common migrant in montane scrub and tamarisk. Fall migration peaks in late August to early September but lasts until late October. A singing male was seen in chokecherry and aspens in the middle fork of Coal Mine Wash on 26 May 1986.

Yellow-breasted Chat (***Icteria virens***). A sparse transient. One was seen in tamarisk on Moenkopi Wash on 27 August 1990, and another in tamarisk 25 May–8 June 1993.

Western Tanager (***Piranga ludoviciana***). A common migrant throughout the area in pinyon-juniper and tamarisk. A common summer resident in mixed-conifer of the upper canyons. Records range from 2 May (1985) to 25 September (1986). A pair was seen attending a nest in Yellow Water Canyon on 15 June 1986. Another pair was feeding nestlings in Coal Mine Wash on 27 June 1989. The last spring migrants are seen in early June. Fall migrants are seen away from the breeding habitat beginning in mid-July.

Black-headed Grosbeak (***Pheucticus melanocephalus***). A common migrant and summer resident in aspen groves and mixed-conifer of the upper canyons. Migrants are occasionally seen in tamarisk. A pair was seen building a nest in the east fork of Coal Mine Wash on 24 June 1984, and three family groups were seen on 2 July 1992. Woodbury and Russell (1945) report collecting a male. The breeding form is *P. m. melanocephalus*.

Blue Grosbeak (***Guiraca caerulea***). A common summer resident in tamarisk on Moenkopi, Coal Mine, and Red Peak Valley washes. Two fledglings were seen below J-7 dam on 29 August 1985. Another was seen on 30 August 1989. This is the most numerous breeding bird of the tamarisk thickets along the lower washes. A transect breeding density of about 11 pairs/40 ha was determined in late June 1986 on Moenkopi Wash. *G. c. interfusa* is the breeding form.

Lazuli Bunting (***Passerina amoena***). A common fall migrant from mid-August to early October in tamarisk of the large washes. Less common elsewhere. On 12 September 1985, 19.5 individuals/40 ha were counted on Moenkopi Wash. Up to five males and two females were present in Russian olives on Moenkopi Wash throughout the summer of 1992. A sixth singing male was at the mouth of Yucca Flat Wash on 15 June 1992. An adult female with a fledgling was seen in the olives on 14 July 1992.

Indigo Bunting (***Passerina cyanea***). A sparse transient. A singing (but nonbreeding) adult male was seen in tamarisk on Moenkopi Wash near the Yucca Flat Wash confluence on 26–27 June 1990. A male paired with a female Lazuli Bunting bred successfully (fledgling seen 29 July) in Russian olives on Moenkopi Wash in 1992.

Green-tailed Towhee (***Pipilo chlorurus***). A common migrant in tamarisk and brush along the major washes and less commonly elsewhere. A common summer resident in Gambel oaks in chained pinyon-juniper on Lolomai and Kayenta points. Also found breeding on Lolomai Point in an undisturbed basin of big sage and wax currant bordered by Gambel oak and chokecherry. Spring migrants appear in mid-April. Most are gone in fall by late September. Nearly 80 individuals/40 ha were counted on Moenkopi Wash on 12 September 1985.

Rufous-sided Towhee (***Pipilo erythrophthalmus***). A common summer resident in montane scrub in mixed-conifer of the upper canyons. A fairly common summer resident in high-elevation pinyon-juniper with a heavy big sage understory or in areas with Gambel oak. Small numbers winter in Russian olives on Moenkopi Wash. Migrates widely throughout the area. A nest with four eggs was found at the head of the west fork of Coal Mine

Wash on 23 May 1983. Small fledglings have been seen in late June. An individual in first pre-basic molt was seen on 2 September 1986. Towhees are actively singing in the upper canyons in early March. A spot-map density from dense pinyon-juniper in White House Valley indicated 3.8 pairs/40 ha. The breeding form is *P. c. montanus.*

American Tree Sparrow (***Spizella arborea***). A sparse winter resident. One record: a single bird was seen on Moenkopi Wash on 1 December 1992.

Chipping Sparrow (***Spizella passerina***). A common summer resident in pinyon-juniper and open mixed-conifer areawide. Records span from 1 April (1982) to 2 November (1990). Nest building was observed on 31 May (1983), small young (5–7 days) were found on 19 June 1984 and 21 June 1983, and fledglings or full-sized juveniles have been seen from 19 June (1983) to 30 July (1985). Flocks begin forming in mid-July and have been seen until mid-October. Pinyon-juniper transect densities range from 2.6 to 42.7 individuals/40 ha. Spot-map breeding densities in pinyon-juniper range from 7.6 to 11.5 pairs/40 ha. The breeding form is *S. p. arizonae.*

Brewer's Sparrow (***Spizella breweri***). A common summer resident in sagebrush and saltbush. Observed from 10 April (1984) to 17 October (1985). Individuals have been noted singing on 22 April (1983), nest building has been seen on 4 May (1982), nests with eggs have been found on 26 May (1983) and 27 May (1985), nestlings were found on 4 June 1984, and fledglings have been seen 4–27 July. Flocks begin forming in late July and have been seen until mid-October. Brewer's Sparrows are abundant in tamarisk in September on the larger washes. Transect densities range from 0.4 to over 500 individuals/40 ha. Spot-map breeding densities are 3.0–8.9 pairs/40 ha in mixed-shrub shrubland and 3.3 pairs/40 ha in a reclaimed area with well-developed saltbush (4700 shrubs/ha). The nominate form is the breeding bird.

Clay-colored Sparrow (***Spizella pallida***). A sparse transient. One was seen on Moenkopi Wash on 4 September 1992.

Vesper Sparrow (***Pooecetes gramineus***). A common migrant in open terrain throughout the area. Less numerous as a breeding resident. Records span from 9 March (1983) to mid-November. Breeding is documented by nests with eggs found in heavily grazed saltbush in upper Reed Valley on 6 May 1982 and in N-2 reclaimed area on 25 May 1992. It may breed in other open shrublands and in chained pinyon-juniper on the mesa summit. Transect densities range from 0.9 to 27.5 individuals/40 ha. Monson and Phillips (1981) assign the breeding form to *P. g. altus*, but Behle (1985) calls it *P. g. confinis.*

Lark Sparrow (***Chondestes grammacus***). A common summer resident in greasewood, open mixed-shrub, juniper savanna, and less numerously in open pinyon-juniper. Lark Sparrows seen in the Lolomai Point chaining on 14 July 1984 and 27 June 1985 may not breed there. Adults feeding two young still in the nest were seen on 24 June 1988. A fledgling was seen at the mesa foot on 19 June 1986. Flocks begin forming in late July. Records range from mid-April to early September. The breeding form is *C. g. strigatus.*

Black-throated Sparrow (***Amphispiza bilineata***). A common summer resident of the lower washes in greasewood and adjacent shadscale-covered terraces and in mixed-shrub habitats containing greasewood and/or shadscale. Transient individuals have been seen in pinyon-juniper and reclaimed areas. A nest with three eggs was found in a shadscale bush on lower Moenkopi Wash on 19 June 1989. Records span from early April to early September. Transect densities range from 1.8 to 12.4 individuals/40 ha. Spot-map densities in mixed-shrub for 1984 and 1985 are 11.9 and 5.9 pairs/40 ha, respectively. Perhaps strong competitive pressure from large numbers of Chipping, Brewer's and Vesper Sparrows in late August and early September accounts for the abrupt late-summer departure of this species from the area. The breeding form is *A. b. deserticola.*

Sage Sparrow (***Amphispiza belli***). A common late-winter to early fall resident of sagebrush, saltbush, and mixed-shrub terrains. Small numbers winter in saltbush at the mesa foot and in lower Moenkopi Wash where 12 were seen on 13 December 1989. Usually first seen on the lease in late February when singing is frequent. Nest building was noted on 6 April 1982. Nests with eggs have been found from late May to late June. Fledglings were noted on 19 June and 23 July 1982. Shrubland transect densities range from 2.7 to 22.9 individuals/40 ha. Spot-map densities for two years in mixed-shrub are 7.4 and 3.0 pairs/40 ha. *A. b. nevadensis* is the breeding form.

Lark Bunting (***Calamospiza melanocorys***). A sparse spring migrant. A male was seen at J-3 reclaimed area on 19 May 1983.

Savannah Sparrow (***Passerculus sandwichensis***). A common migrant in weedy pond and stream edges. Spring observations range from mid-March (27 February 1989 being early) through April; one seen 25 May 1992 in N-2 reclaimed area was exceptionally late. Fall records are from mid-July to mid-October.

Song Sparrow (***Melospiza melodia***). A fairly common migrant in tamarisk along the major washes and at weedy pond edges. It winters in small numbers in the same areas.

Lincoln's Sparrow (***Melospiza lincolnii***). A fairly common fall migrant at weedy pond edges and in tamarisk. Very few have been seen in spring.

Swamp Sparrow (***Melospiza georgiana***). A sparse migrant. A single bird in alternate plumage was seen in weeds at a pond in the N-2 reclaimed area 25–27 April 1990.

White-throated Sparrow (***Zonotrichia albicollis***). An adult male was seen with a flock of juncos in an oak thicket in chained pinyon-juniper woodland on Lolomai Point by Gale Monson on 4 November 1990. Another adult was on Moenkopi Wash on 24 April 1992.

White-crowned Sparrow (***Zonotrichia leucophrys***). A common migrant in brush and tamarisk throughout the length of the major washes. Also common in brushy chained pinyon-juniper on Lolomai Point. This species became markedly more numerous in the 1980s as a winter resident in tamarisk and adjacent greasewood thickets along the lower washes. Indicative of this increase was a flock of 195 seen in Russian olives on 9 January 1992. One was seen in chained pinyon-juniper on Lolomai Point on 17 June 1983. Transect densities range from 3.5 to 134.8 individuals/40 ha.

Harris' Sparrow (***Zonotrichia guerula***). A sparse winter resident. Single individuals were seen in the Russian olive grove on 29 January 1992 and 24 April 1992.

Dark-eyed Junco (***Junco hyemalis***). An abundant winter resident throughout the area but primarily distributed in small flocks along washes. A common summer resident in dense mixed-conifer of the upper canyons. The forms that winter in the area are present from late September to early May. The arrival of fall birds appears to displace the flocks of Chipping and Brewer's Sparrows in tamarisk of the lower washes. The local breeding form apparently winters in the upper canyons where they were segregated from wintering forms on 4 March and 25 September 1984, 26 October 1985, and 16 December 1989. Nests with eggs have been found from 22 May (1983) to 17 June (1985). Fledglings have been seen from 16 June (1982) to 13 July (1983). Full-sized immatures were seen on 30 July 1985, and a bird in pre-basic molt was seen on 14 August 1984. Birds seen in mid-September were all in basic plumage. The breeding form is intermediate between *J. h. dorsalis* and *J. h. caniceps*, which is typical for all juncos that breed in northeastern Arizona (see Woodbury and Russell 1945 and Phillips et al. 1964).

Chestnut-collared Longspur (***Calcarius ornatus***). Primarily a sparse fall migrant recorded only from reclaimed areas. Records include one seen by EH&A Consultants on 9 October 1979, one in J-1/N-6 reclaimed area on 2 October 1985, one at N-2 reclaimed area on 16 October 1989, one at J-7 reclaimed area on 1 October 1990, one at N-2 reclaimed area on 30 October 1990, and up to 10 in N-1 reclaimed area 14–17 October 1991. The only spring occurrence is two males at N-2 reclaimed area on 30 March 1990.

Bobolink (***Dolichonyx oryzivorus***). A sparse migrant. A male in alternate plumage was seen in N-1 reclaimed area on 17 May 1989.

Red-winged Blackbird (***Agelaius phoeniceus***). A common migrant at ponds throughout the area. Small numbers nest at several ponds in the lease area. A flock of about 50 wintered on lower Coal Mine and Moenkopi washes in 1988–89. The breeding race is *A. p. fortis*.

Eastern Meadowlark (***Sturnella magna***). A single bird identified by call, song, and throat color pattern was seen in J-7 reclaimed area 3–4 June 1991.

Western Meadowlark (***Sturnella neglecta***). A common summer resident in reclaimed areas, the highway right-of-way in Long House Valley, the valley of lower Moenkopi Wash, and the J-8 mine plan area. Two nests found in reclaimed areas on 16 May 1989 contained four and five eggs, respectively. Another found on 30 May 1989 held five eggs. Broods typically leave the nest in late May–early June and again in late July–early August. A common migrant in reclaimed areas and occasionally in shrublands. A sparse winter resident in reclaimed areas, not returning in numbers until early March. From 2.2 to 3.3 pairs/40 ha have been found in reclaimed areas. The nominate race breeds.

Yellow-headed Blackbird (***Xanthocephalus xanthocephalus***). A common migrant, usually near ponds, throughout the area. Most records are from April and from mid-July to October. A single male was noted at N-1 reclaimed area on 24 June 1992.

Brewer's Blackbird (***Euphagus cyanocephalus***). A common migrant at ponds throughout the area. Small numbers breed at J-7 and other ponds. Also breeds in small numbers in moist tamarisk sites on Moenkopi Wash. A female feeding fledglings was seen at J-7 pond on 5 July 1985 and at a pond in N-2 reclaimed area on 19 July 1985. A pair feeding small young was seen on 10 June 1986 at a pond in N-2 reclaimed area.

Great-tailed Grackle (***Quiscalus mexicanus***). A sparse migrant. Three males and a female were seen in J-27 reclaimed area on 23 April 1984, a single male was seen at a pond on 5 May 1989, and another lone male was seen on 18 June 1990.

Brown-headed Cowbird (***Molothrus ater***). A common summer resident in small numbers throughout the area, the largest group being a migrant flock of 147 birds seen on 24 April 1992. Records span from late April to mid-September. Black-throated Gray Warblers are the only host species noted from the area. Transect densities range from 0.4 to 8.9 individuals/40 ha. *M. a. artemisiae* and *M. a. obscurus* overlap in northeastern Arizona. Probably sparse or absent in the study area before the 1930s (Woodbury and Russell 1945).

Northern Oriole (***Icterus galbula***). A common fall migrant in tamarisk from early August to mid-September. Less numerous in the spring. A male was seen in pinyon-juniper woodland on 11 May 1982. Two were seen in tamarisk on lower Coal

Mine Wash on 27 May 1986. Another was seen in the same area on 23 June 1986. A female was seen in aspens in the middle fork of Coal Mine Wash on 26 May 1986.

Scott's Oriole (***Icterus parisorum***). A common summer resident of juniper savanna and open pinyon-juniper. Records range from 23 April (1993) to 13 August (1986 and 1992). A pair with two small fledglings was seen in the J-8 mine plan area on 18 June 1986. This species possesses large territories; four closely observed pairs (including the above) had territories averaging 51.6 ha/pair (127 ac/pair) in June 1986.

FAMILY FRINGILLIDAE

Rosy Finch (***Leucosticte arctoa***). A sparse winter resident. On 3 January 1984 four individuals of a "gray-crowned" form were seen feeding on Russian thistle seeds on a shadscale-covered Mancos Shale slope on lower Moenkopi Wash.

Pine Grosbeak (***Pinicola enucleator***). A sparse winter resident. Seven were seen in mixed-conifer on 1 November 1992. Two females were seen feeding on quaking aspen buds at the head of Yellow Water Canyon on 12 April 1985. On 4 January 1986, 22 females were seen in pinyon-juniper and Douglas fir on the mesa rim at Kayenta Point. B. Mellberg reported a pair in the east fork of Coal Mine Wash on 17 December 1988 in mixed-conifer.

Cassin's Finch (***Carpodacus cassinii***). A fairly common to common winter resident in wooded terrain throughout the area. It is absent some years. Singing and displaying males on Lolomai Point on 12 April 1985, singing males on 14 June 1984 and 25 June 1986, and a male foraging and carrying food on 23 June 1988 may indicate breeding near the rim in mixed-conifer habitats.

House Finch (***Carpodacus mexicanus***). A common permanent resident throughout the area. Retreats in winter to lower elevations. Fledglings have been seen on 22 July and 11 August 1982. G. Swan found a new nest under the cowling of his Cessna on 3 May 1985, suggesting that the nest causing an exciting engine failure in J. Gibbs' Cessna four years earlier was also from this species. Transect densities range from 0.4 to 53.3 individuals/40 ha. Spot-map densities in pinyon-juniper are all 3.8 pairs/40 ha. *C. m. frontalis* is the breeding form. Flocks of up to 300 winter on lower Moenkopi Wash.

Red Crossbill (***Loxia curvirostra***). An irregularly common permanent resident in mixed-conifer in the upper canyons. Frequently seen in dense pinyon-juniper woodland away from the rim area. Very young fledglings were seen in mixed-conifer in Coal Mine Wash on 10 March 1989. Several family groups were noted in upper Moenkopi Wash on 2 May 1989. Another family group was seen in Yellow Water Canyon on 5 May 1992. For the complex of races in the region, see Monson and Phillips (1981).

Pine Siskin (***Carduelis pinus***). A common winter resident throughout the area, more numerous in the spring. Over 300 were seen feeding on dandelion seeds (*Taraxacum officinale*) in a side canyon of Moenkopi Wash on 24 May 1985. Breeding by birds seen fairly commonly in summer in mixed-conifer is unconfirmed. Seemingly more numerous in 1992, at which time it wandered widely during the summer throughout the area, with birds noted in tamarisk on 23 and 29 July, 5 August; 30 were seen in thistles (*Cirsium vulgare*) at Pond J28-G on 18 August. If breeding occurs, Monson and Phillps (1981) would assign them to the nominate form. Behle (1985) assigns birds in the region to *C. p. vagran.*

Lesser Goldfinch (***Carduelis psaltria***). A common summer resident throughout the area. Most are seen from late April to early December. During October they feed extensively on seeds of threadleaf groundsel (*Senecio longilobus*), as a flock of 35+ were observed doing on 4–5 October 1989. Fledglings were seen on 13 July 1986. The nominate race is the breeding form, and both black-backed and green-backed males are frequently observed.

American Goldfinch (***Carduelis tristis***). Irregularly common from early September to mid-May. It frequents weedy roadsides throughout the area. These birds are most numerous from December to mid-May. Males usually undergo pre-alternate molt in April and early May before disappearing.

Evening Grosbeak (***Coccothraustes vespertinus***). An uncommon fall migrant with most records being from early October into January. Spring records include two on 14 April 1985, 27 on 29 April 1991, and many widespread flocks in March–April 1993. Nearly 50 were seen feeding on Russian olive fruit on lower Moenkopi Wash on 13 December 1989 and four were seen there on 3 January 1991.

FAMILY PASSERIDAE

House Sparrow (***Passer domesticus***). A common permanent resident at mine shops and facilities. This species was probably absent from the area prior to mine development.

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APPENDIX 1. Bird species recorded on northern Black Mesa, Arizona.

Common name and breeding status[a]	Seasonal status[b]	Habitat preference[c]	Relative seasonal abundance[d]			
			Spring	Summer	Fall	Winter
Common Loon	M	P	F	S	S	—
Pied-billed Grebe*	M	P	C	U	C	C
Horned Grebe	M	P	S	—	—	S
Eared Grebe	M	P	C	U	C	C
Western Grebe	M	P	F	U	F	—
American White Pelican	M	P	S	S	S	—
Double-crested Cormorant	M	P	—	S	—	—
Great Blue Heron	M	P	C	C	C	U
Great Egret	M	P	—	—	S	—
Snowy Egret	M	P	C	C	C	—
Cattle Egret	M	P	S	S	S	—
Black-crowned Night-Heron	M	P	F	F	F	—
White-Faced Ibis	M	P	C	F	C	—
Snow Goose	M	P	—	—	S	S
Ross' Goose	M	P	S	—	S	—
Canada Goose	M,W	P, Rc	U	S	U	F
Wood Duck	M	P	—	—	—	S
Green-winged Teal	M	P	A	U	C	C
Mallard*	P	P	C	C	C	C
Northern Pintail*	M,S	P	U	C	F	F
Blue-winged Teal	M	P	U	S	—	—
Cinnamon Teal?*	M	P	C	C	C	C
Northern Shoveler	M	P	C	S	C	U
Gadwall	M	P	C	C	C	U
Eurasian Wigeon	M	P	S	—	S	S
American Wigeon	M	P	F	—	F	F
Canvasback	M	P	U	S	U	S
Redhead	M	P	C	S	C	C
Ring-necked Duck	M,W	P	C	—	C	C
Greater Scaup	M	P	S	—	—	—
Lesser Scaup	M	P	C	—	C	C
White-winged Scoter	M	P	—	—	S	—
Common Goldeneye	M	P	S	—	—	—
Bufflehead	M	P	F	S	C	U
Hooded Merganser	M	P	S	—	S	S
Common Merganser	M	P	F	S	F	S
Red-breasted Merganser	M	P	U	—	S	—
Ruddy Duck	M	P	C	C	C	F
Turkey Vulture?*	S	Ct	C	C	C	—
Osprey	M	P, To	F	S	F	—

APPENDIX 1. Continued.

Common name and breeding status[a]	Seasonal status[b]	Habitat preference[c]	Relative seasonal abundance[d]			
			Spring	Summer	Fall	Winter
Bald Eagle	M	Mc,PJ	S	—	—	S
Northern Harrier	W	To	F	U	F	U
Sharp-shinned Hawk*	P	A,Mc,PJ	C	F	C	U
Cooper's Hawk*	P	Mc,PJ,A	C	C	C	U
Northern Goshawk*	P	Mc,PJ	F	S	F	F
Swainson's Hawk	M	Ms, Pc	S	S	S	—
Red-tailed Hawk*	P	Ct,PJ,Mc	C	C	C	C
Ferruginous Hawk	M	Ms	U	S	U	U
Rough-legged Hawk	W	Rc	S	—	S	S
Golden Eagle*	P	Ct	S	S	S	S
American Kestrel*	P	Pc,Ct,PJ	C	C	C	U
Merlin	W	Js,Ms	S	—	F	F
Peregrine Falcon*	M	Rc,PJ	S	S	S	—
Prairie Falcon*	P	Ct	U	U	U	U
Chukar?*	P	Ct	S	S	S	S
Wild Turkey	AR	—	—	—	—	—
Northern Bobwhite	AR	—	—	—	—	—
Scaled Quail	AR	—	—	—	—	—
Gambel's Quail	AR	—	—	—	—	—
American Coot*	M,S	P	C	C	C	F
Sora	M	P	S	S	S	—
Sandhill Crane	AR	—	—	—	—	—
Semipalmated Plover	M	P	S	—	—	—
Killdeer*	P	P,Ri	C	C	C	F
Black-necked Stilt	M	P	U	U	—	—
American Avocet	M	P	U	U	U	—
Greater Yellowlegs	M	P	F	U	F	—
Lesser Yellowlegs	M	P	C	F	C	—
Solitary Sandpiper	M	P	U	F	F	—
Willet	M	P	F	U	F	—
Spotted Sandpiper?*	M,S	P	C	F	C	—
Long-billed Curlew	M	P	S	S	—	—
Marbled Godwit	M	P	F	—	—	—
Western Sandpiper	M	P	C	C	C	—
Least Sandpiper	M	P	C	C	C	—
Baird's Sandpiper	M	P	—	S	F	—
Pectoral Sandpiper	M	P	—	S	S	—
Long-billed Dowitcher	M	P	F	U	F	—
Common Snipe	M	P,Ri	F	S	F	S
Wilson's Phalarope	M	P	C	S	S	—
Red-necked Phalarope	M	P	U	S	S	—
Franklin's Gull	M	P	U	—	—	—
Bonaparte's Gull	M	P	F	—	S	—
Ring-billed Gull	M	P	C	F	F	—
California Gull	M	P	U	—	U	—
Herring Gull	M	P	S	—	—	—
Common Tern	M	P	S	S	S	—
Forster's Tern	M	P	F	S	S	—
Black Tern	M	P	—	S	S	—
Rock Dove	T	PJ	—	S	S	—
Band-tailed Pigeon	T	Pc	—	S	—	—
Mourning Dove*	S	Rc,PJ	C	C	C	S
Greater Roadrunner	P	G,Ri	S	S	S	S
Flammulated Owl*	M	PJ,Mc	U	U	S	—
Western Screech-Owl?*	P	PJ,Mc	U	U	U	U
Great Horned Owl*	P	Ct,Mc	F	F	F	F
Northern Pygmy-Owl?*	P	Mc	U	U	F	F
Burrowing Owl	Ar	—	—	—	—	—
Spotted Owl*	P?	Mc,Ct	F	F	F	F
Long-eared Owl*	P	PJ,Mc	S	S	—	—
Northern Saw-whet Owl	S	Mc	S	S	—	S

APPENDIX 1. Continued.

Common name and breeding status[a]	Seasonal status[b]	Habitat preference[c]	Relative seasonal abundance[d]			
			Spring	Summer	Fall	Winter
Common Nighthawk*	S	PJ	—	C	F	—
Common Poorwill?*	S	PJ	U	U	U	—
White-throated Swift*	S	Ct	C	C	C	—
Black-chinned Hummingbird*	S	PJ,Mc	C	C	C	—
Calliope Hummingbird	M	PJ	—	S	—	—
Broad-tailed Hummingbird*	S	Mc	C	C	—	—
Rufous Hummingbird	M	PJ	—	C	C	—
Belted Kingfisher	M	P	F	F	F	—
Lewis' Woodpecker*	M	Pc	F	F	F	S
Acorn Woodpecker?*	S	Pc	U	F	F	—
Red-naped Sapsucker	M	Mc	F	—	C	S
Williamson's Sapsucker*	M	Mc	F	U	F	U
Downy Woodpecker*	P	A,Ri	S	S	S	S
Hairy Woodpecker*	P	A,PJ,Mc	C	C	C	C
Northern Flicker*	P	Ct,PJ,Mc	C	C	C	C
Olive-sided Flycatcher	M	PJ	U	U	—	—
Western Wood-Pewee?*	M,S	Ri,Mc	C	S	C	—
Willow Flycatcher	M	Ri	—	S	S	—
Hammond's Flycatcher	M	Ri	S	—	S	—
Dusky Flycatcher*	S	Mc	C	C	—	—
Gray Flycatcher*	S	PJ,Mc	C	C	C	—
Cordilleran Flycatcher*	S	Ct,Mc	C	C	F	—
Black Phoebe	T	Ri	—	S	—	—
Say's Phoebe*	S	Ct,Ms	C	C	C	S
Ash-throated Flycatcher*	S	PJ,Mc	C	C	—	—
Cassin's Kingbird*	S	PJ	C	C	U	—
Western Kingbird*	S	PJ	F	F	C	—
Eastern Kingbird	M	Rc	—	S	—	—
Scissor-tailed Flycatcher	T	Js	—	S	—	—
Horned Lark*	P	Sg,St,Rc,Js,Ms	A	A	A	A
Purple Martin	M	Ms	—	S	S	—
Tree Swallow	M	P	C	C	C	—
Violet-green Swallow*	S	Ct,PJ,Mc	C	C	C	—
Northern Rough-winged Swallow*	S	Ct	C	C	C	—
Bank Swallow	M	P	C	C	C	—
Cliff Swallow*	M	Ct	C	U	C	—
Barn Swallow*	M	P	C	U	C	—
Steller's Jay*	P	Mc	C	C	C	C
Scrub Jay*	P	S,PJ,Mc	C	C	C	C
Pinyon Jay*	P	PJ,Mc	C	C	C	C
Clark's Nutcracker*	P	Mc	C	C	C	C
American Crow	T,AR	Ms	S	—	S	—
Common Raven*	P	Ct,PJ,Mc	A	A	A	A
Mountain Chickadee*	P	PJ,Mc	C	C	C	C
Plain Titmouse*	P	PJ,Mc	C	C	C	C
Bushtit*	P	PJ,Mc,Ri	C	C	C	C
Red-breasted Nuthatch*	W,S	Mc	C	U	C	C
White-breasted Nuthatch*	P	PJ,Mc	C	C	C	C
Pygmy Nuthatch*	P	Mc	C	C	C	C
Brown Creeper*	P	Mc	F	F	F	F
Rock Wren*	S	Ms,Ct,PJ	C	C	F	S
Canyon Wren*	P	Ct,PJ,Mc	C	C	C	F
Bewick's Wren*	P	PJ,Mc	C	C	C	C
Winter Wren	T	A	—	—	S	—
House Wren*	M,S	A	C	C	C	—
Marsh Wren	M	P	F	—	F	—
Golden-crowned Kinglet	W	Mc	U	—	F	F
Ruby-crowned Kinglet?*	M	Mc	C	C	C	S
Blue-gray Gnatcatcher*	S	PJ,Mc	C	C	C	—
Western Bluebird*	P	PJ,Mc	C	C	C	U
Mountain Bluebird*	P	Pc,PJ,Mc	C	C	C	F

APPENDIX 1. Continued.

Common name and breeding status[a]	Seasonal status[b]	Habitat preference[c]	Relative seasonal abundance[d]			
			Spring	Summer	Fall	Winter
Townsend's Solitaire*	P	A,Ct,Mc	C	F	C	C
Hermit Thrush*	S	A,Mc	C	C	C	—
Varied Thrush	T	Ri	—	—	S	—
American Robin*	P	A,Mc	C	F	C	U
Northern Mockingbird*	S	G,Js,Ms	C	C	—	—
Sage Thrasher*	S	Sg,St,Rc,Mx	C	C	C	—
Bendire's Thrasher*	S	G,Js,Ms	F	F	—	—
American Pipit	W	P	C	U	C	S
Bohemian Waxwing	T	PJ	S	—	S	—
Cedar Waxwing	M	PJ	S	S	S	S
Northern Shrike	W	PJ,Sa	S	—	S	F
Loggerhead Shrike*	P	G,Js,Ms	C	C	C	F
European Starling*	P	Ms	C	C	C	C
Gray Vireo*	S	PJ	F	F	F	—
Solitary Vireo*	S	PJ,Mc	C	C	C	—
Warbling Vireo*	M,S	A	C	C	C	—
Tennessee Warbler	M	Ri	—	—	S	—
Orange-crowned Warbler*	M,S	S,A,Mc	C	F	C	—
Nashville Warbler	M	Ri	—	C	C	—
Virginia's Warbler*	S,M	S,Pc,A,Mc	C	C	C	—
Lucy's Warbler	T	Ri	S	—	—	—
Yellow Warbler	M	Ri,A	S	C	C	—
Yellow-rumped Warbler*	M,S	Mc	C	F	A	F
Black-throated Gray Warbler*	S	PJ,Mc	C	C	C	—
Townsend's Warbler	M	Mc,Ri	—	F	C	—
Hermit Warbler	M	Ri	—	—	S	—
Grace's Warbler*	S	Mc	C	C	F	—
American Redstart	T	PJ	—	S	—	—
Northern Waterthrush	M	P	S	—	S	—
Kentucky Warbler	T	S,Ri	S	—	S	—
MacGillivray's Warbler*	M	S,A	C	C	C	—
Common Yellowthroat	M	P,Ri	S	F	F	—
Wilson's Warbler	M	Ri	C	C	C	—
Yellow-breasted Chat	M	Ri	S	S	—	—
Western Tanager*	S,M	Mc	C	C	C	—
Black-headed Grosbeak*	M,S	A,Mc	C	C	F	—
Blue Grosbeak*	S	Ri	C	C	C	—
Lazuli Bunting*	M,S	Ri	F	C	C	—
Indigo Bunting*	S	Ri	S	S	—	—
Green-tailed Towhee*	M,S	Pc,Sg	C	C	C	—
Rufous-sided Towhee*	P	S,Pc,PJ,Mc	C	C	C	F
American Tree Sparrow	W	Ri	—	—	—	S
Chipping Sparrow*	S	Js,Pc,PJ,Mc	C	C	C	—
Brewer's Sparrow*	S,M	Sg,St,Rc,Pc,G	C	C	C	—
Clay-colored Sparrow	T	Ri	—	—	S	—
Vesper Sparrow*	M,S	St,Mc,Pc	C	C	C	—
Lark Sparrow*	S	G,Rc,Js,Ms	C	C	C	—
Black-throated Sparrow*	S	G,Ms	C	C	S	—
Sage Sparrow*	P	Sg,St,Ms	C	C	C	F
Lark Bunting	M	Rc	S	—	—	—
Savannah Sparrow	M	P	C	C	C	U
Song Sparrow	M,W	Ri	F	—	F	U
Lincoln's Sparrow	M	Ri	F	—	F	—
Swamp Sparrow	M	Ri	S	—	—	—
White-throated Sparrow	M	Pc	S	—	S	—
White-crowned Sparrow	M	Ri,S	C	S	A	C
Harris' Sparrow	W	Ri	S	—	—	S
Dark-eyed Junco*	W,S	A,Mc	C	C	C	A
Chestnut-collared Longspur	M	Rc	S	—	S	—
Bobolink	M	Rc	S	—	—	—
Red-winged Blackbird	M	P	C	C	C	U

APPENDIX 1. Continued.

Common name and breeding status[a]	Seasonal status[b]	Habitat preference[c]	Relative seasonal abundance[d]			
			Spring	Summer	Fall	Winter
Eastern Meadowlark	M?	Rc	—	S	—	—
Western Meadowlark*	P	Rc,Js,Ms	C	C	C	U
Yellow-headed Blackbird	M	P	C	C	C	—
Brewer's Blackbird*	S	P,Ri	C	F	C	S
Great-tailed Grackle	M	Rc	S	S	—	—
Brown-headed Cowbird*	S	PJ	C	C	C	—
Northern Oriole	M	Ri,PJ	F	C	F	—
Scott's Oriole*	S	Js,PJ	C	C	—	—
Rosy Finch	W	Ms	—	—	—	S
Pine Grosbeak	W	A,Mc	S	—	S	S
Cassin's Finch?*	W,S	Mc	F	U	C	C
House Finch*	P	Ri,PJ	C	C	C	C
Red Crossbill*	P	Mc	C	C	C	C
Pine Siskin?*	P	Mc	C	F	C	C
Lesser Goldfinch*	S	Ri,PJ	C	C	C	S
American Goldfinch	W	PJ	C	—	C	C
Evening Grosbeak	M	Mc,PJ	—	—	U	—
House Sparrow*	P	Ms	C	C	C	C

[a] Common names follow the sequence and spelling of the American Ornithologists' Union (1983, 1985, 1987, 1989). * = breeding confirmed; ?* = breeding suspected.

[b] M = migrant
W = winter resident
AR = only in archaeological record
S = summer resident
P = permanent resident
T = transient
If two seasonal status listings are given, the principal status is given first.

[c] S = montane scrub
Sg = sagebrush
St = saltbush
G = greasewood
Rc = reclaimed mine spoil
Js = juniper savanna
Ri = riparian habitats
P = ponds
Pc = chained pinyon-juniper
Ms = mixed-shrub
A = aspen groves
Ct = cliffs, talus slopes, wash banks
PJ = pinyon-juniper
Mc = mixed-conifer
If a species is found in two or more habitat types, the principal one is given. If it is found throughout, "To" is designated. If breeding is confirmed or suspected, only the breeding habitat(s) are those listed.

[d] A = abundant
C = common
F = fairly common
U = uncommon
S = sparse
Cs = casual
Ac = accidental

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EFFECTS OF COBBLE EMBEDDEDNESS ON THE MICRODISTRIBUTION OF THE SCULPIN *COTTUS BELDINGI* AND ITS STONEFLY PREY

Roger J. Haro[1,2] and Merlyn A. Brusven[1,3]

ABSTRACT.—Laboratory experiments were undertaken to assess the effects of three levels of cobble embeddedness on the microdistribution of the sculpin *Cottus beldingi* and its stonefly prey, *Skwala americana*. Experiments were conducted separately and together as predator and prey in temperature- and flow-controlled artificial streams. When tested either separately or together, both the predator sculpin and its stonefly prey occurred in significantly greater numbers on substrata having unembedded cobbles than substrata having half- or completely embedded cobbles. Stonefly densities were greater in substrata having unembedded cobbles even though predator densities within the more embedded cobble patches were significantly lower. These findings support the hypothesis that higher predator densities influence prey densities less than the structural habitat quality of unembedded-cobble patches.

Key words: predator-prey, cobble embeddedness, nonlethal effects, stoneflies, sculpins, nonpoint source sedimentation, Cottus beldingi.

Reduced summer flows and increased sedimentation in many western North American streams may significantly diminish the size and availability of adequate microhabitat patches for benthic fish and insects. Sedimentation from agricultural sources has been linked to pronounced changes in the trophic structure of lotic fish assemblages (Berkman and Rabeni 1987) and may affect macroinvertebrate community structure, further altering trophic relations within the lotic food web.

Such trophic changes, in part, may result from alterations in prey refugia brought about by the embeddedness of cobble substrata. Brusven and Rose (1981) found that cobble embeddedness significantly influenced the vulnerability of two insect predators, *Hesperoperla pacifica* (Plecoptera: Perlidae) and *Rhyacophila vaccua* (Trichoptera: Rhyacophilidae), to predation by *Cottus rhotheus*. They suggested high sculpin predation success in the embedded substrata was due to the loss of macroinvertebrate refugia under cobbles.

Microhabitat shifts by macroinvertebrate prey in response to vertebrate and macroinvertebrate predators have been reported by several workers (Stein and Magnuson 1976, Stein 1977, Peckarsky and Dodson 1980, Peckarsky 1983). Feltmate et al. (1986) found that, under laboratory conditions, *Paragnetina media* (Plecoptera: Perlidae) selected larger substrata over smaller ones in the presence of rainbow trout.

Sculpins hold a significant position in the food web of Pacific Northwest stream communities and have been shown to reduce food resources, food consumption, and the production of trout (Brocksen et al. 1968). *Cottus beldingi*, the Paiute sculpin, is the most abundant fish species in Lapwai Creek (Kucera et al. 1983), the stream investigated in this study. This ambush predator feeds almost exclusively on benthic macroinvertebrates (Johnson 1985). Finger (1982) reported that adult *C. beldingi* preferred coarse-grained substrata in an Oregon stream. In California, Gard and Flittner (1974) found the highest densities of *C. beldingi* in rubble or gravel substrata.

Skwala americana (Plecoptera: Perlodidae) is a common lotic stonefly found throughout western North America (Baumann et al. 1977). Nymphs are important prey of *C. beldingi* (Johnson 1985) and are normally found in relatively unsedimented, unembedded-cobble riffles (Short and Ward 1980). They commonly feed on small mayflies and midges (Fuller and Stewart 1977, Richardson and Gaufin 1971). *Skwala americana* is univoltine, with adult

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emergence occurring from February through July (Baumann et al. 1977).

The purpose of this study was to determine the microdistribution of *C. beldingi* and *Skwala americana*, both separately and together as predator and prey, when given choices among three levels of cobble embeddedness in an artificial stream.

MATERIALS AND METHODS

Field Collection

Lapwai Creek (46°18'N, 116°43'W) drains agricultural land in the Columbia River Basin 20 km east of Lewiston, Idaho. Field estimates of sculpin density were made in September 1987 from riffles in Lapwai Creek and its tributaries. Sculpins were frightened into a drift net attached to two wire-mesh sidewings that sampled a rectangular 0.44-m^2 area. Adult sculpins (66.1 ± 9.4 mm) used in the experiment were collected during September and October 1987.

Late-instar stonefly nymphs (*Skwala americana*) were collected with kick nets from the same riffles from which sculpins were collected. The nymphs were transported to the laboratory.

Preconditioning of Test Organisms

Sculpins and stoneflies were acclimated in laboratory streams like those described by Brusven (1973). Cobbles were placed in the streams to provide cover. All organisms were acclimated for at least 48 h in holding streams before each experiment. Sculpins were randomly selected 24 h before each experiment, isolated, and starved to better elicit hunger and foraging behavior.

Experimental Stream Channels

Two Plexiglas® streams (3.35 × 0.25 × 0.20 m) were arranged side by side in the laboratory. The streams were partitioned into three 0.19-m^2 sections bordered by a 0.04-m^2 sand area at each end (Fig. 1).

Unchlorinated tapwater was recirculated through the channels by electrical pumps (mean velocity, 2.44 cm s^{-1}). Water temperature was maintained at 13.9°C with thermostatic refrigeration units placed within recirculating sumps. Water depth was held at 13.0 cm above the base substrate, thus assuring that all cobbles were fully submersed.

Substrate Treatments

Natural stream cobbles (62.0–127.0 mm, principal axis) were collected from Lapwai Creek. Cobbles were scrubbed with a brush under hot tap water, dried, and labeled with an identification number and orientation arrow to enable replication of their spatial arrangement in either an unembedded or half-embedded condition. Fifteen cobbles were randomly positioned in each of the test sections of the stream except for the simulated, fully embedded condition, which had no visible surface presence of cobbles. The cobbles covered ca. 60% of the two-dimensional area of the unembedded and 50%-embedded sections.

To simulate a 50%-embedded condition, half of each cobble's principal axis was cast in plaster of paris. The casts were later filled with a mixture of concrete and natural stream sand. After drying, the "half-casts" were textured with a wire brush and assigned an identification number and directional arrow that corresponded to their natural-rock counterparts.

Two centimeters of washed stream sand was spread over the bottom of each artificial stream to serve as a base substratum. Three cobble-embeddedness conditions were randomly assigned among three stream sections. In one section cobbles were placed on top of the sand. In another section the "half-casts"

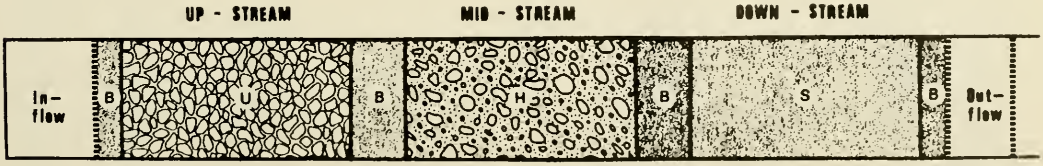

Fig. 1. Schematic diagram of an artificial channel showing the stream sections and one cobble-embeddedness arrangement: (U) = unembedded cobbles, (H) = 50%-embedded cobbles, (S) = 100%-embedded cobbles, and (B) = sand buffer zones.

were positioned in the identical arrangement and orientation as their natural unembedded counterparts. They were placed directly on the sand, thereby limiting access to their under surfaces by the organisms studied. The remaining section was left as a 2.0-cm layer of sand and simulated a 100% cobble-embedded condition with no cobbles evident on the surface.

Experimental Trials

Experimental trials ran for 20 h and were terminated at sunrise (photoperiod, 9 light: 11 dark). Upon completion of a trial, water flow was shut off and partitions were placed between stream sections. Test organisms were recovered from each section and counted. Animals recovered from the buffer sections were not included in the statistical analysis. Two experiments were conducted: (1) predator and prey were tested independently to assess noninteractive distribution, and (2) predator and prey were tested together to assess interactive distribution.

PREDATOR AND PREY—NONINTERACTIVE.—This experiment examined habitat selection by the predator (sculpin) and prey (stonefly) in absence of each other. Two parallel streams were used, one for the predator and one for the prey. Equal numbers of sculpins (2) and stoneflies (4) were introduced into each section (3 sections/stream) of the respective streams and allowed to freely distribute among the sections for 20 h. Sculpin stocking density in the artificial channel (6 fish/channel) approximated sculpin density in the field, i.e., 6.9 fish m^{-2} (Haro 1988).

Three cobble-embedded conditions were randomly assigned among stream sections (i.e., upstream, midstream, and downstream). Each possible cobble arrangement was replicated randomly in time (three times) for a total of nine trials for each organism. A nonparametric Kruskal-Wallis test with a posteriori pairwise comparisons (Conover 1980) was used to detect significant differences among mean-ranked numbers of organisms recovered from three cobble-embeddedness conditions (Conover 1980).

PREDATOR AND PREY—INTERACTIVE.—This experiment examined predator-prey interaction when both the predator and prey were introduced into a common stream. Four stoneflies were placed into each of three sections 1 h prior to the introduction of sculpins (2/section, 6/stream). In this experiment, trials were run concurrently in two parallel streams. Each possible cobble arrangement (three) was replicated in time (four times) for a total of 24 trials. This experiment assessed whether distribution of either the sculpin predator or its prey was altered in the presence of the other species. Statistical tests similar to those described in the first experiment were used to detect significant differences among mean-ranked numbers of organisms from three cobble-embeddedness conditions.

RESULTS

Predator and Prey—Noninteractive

Sculpin numbers (Table 1) were significantly different between substrate-embeddedness conditions ($P < .001$) when tested in absence of stonefly prey. Multiple comparisons showed that mean-ranked sculpin

TABLE 1. Kruskal-Wallis test statistic (T) and mean-ranked sculpin and stonefly counts (R_i/n_i) among cobble-embeddedness conditions. Unique lowercase letters denote significantly different counts within both noninteractive and interactive predator and prey experiments.

	Sculpin		Stonefly	
Treatment	T	R_i/n_i	T	R_i/n_i
Noninteractive ($n_i = 18$)	53.03***		53.16***	
Unembedded		4.88a		8.06a
50%-embedded		1.50b		3.17b
100%-embedded		1.33b		1.39c
Interactive ($n_i = 24$)	71.05***		71.10***	
Unembedded		5.83a		5.63a
50%-embedded		1.58b		2.75b
100%-embedded		1.38b		1.33c

***Kruskal-Wallis test error rate: $P \leq .0001$. Multiple comparison error rate: $P \leq .005$.

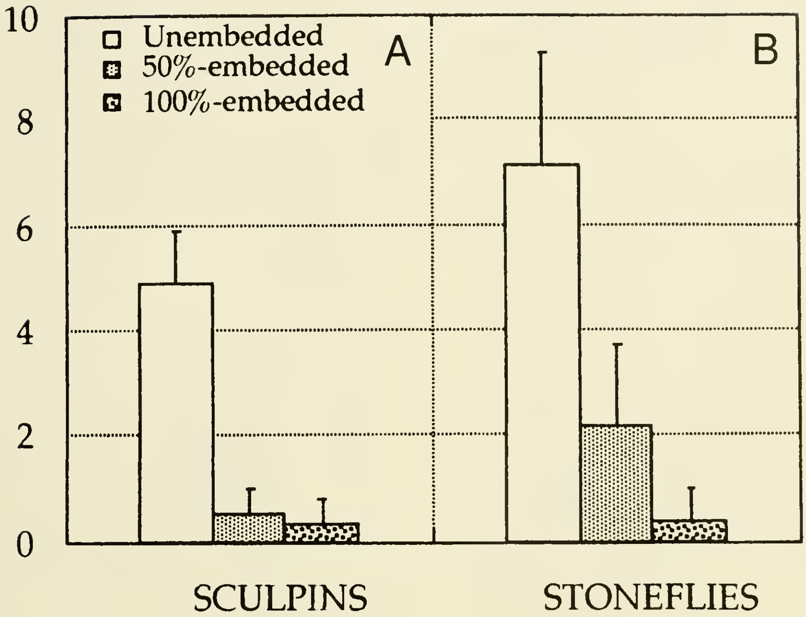

Fig. 2. Mean numbers of (A) *Cottus beldingi* and (B) *Skwala americana* recovered from three cobble-embeddedness conditions ($n = 18$) when tested noninteractively in separate stream channels. Vertical lines indicate 1 SD.

numbers in unembedded-cobble sections were significantly greater ($P < .005$) than in either the 50%- or 100%-embedded sections (Table 1, Fig. 2A); however, there was no difference in ranked sculpin numbers between the latter cobble-embedded conditions. When substrate effects were discounted, no differences were found when sculpin numbers were analyzed by stream section.

Ranked stonefly numbers were also significantly different among substrate-embeddedness conditions ($P < .001$) when tested in absence of sculpin predators (Table 1). Furthermore, all multiple comparisons between substrate conditions were significant ($P < .005$). Like sculpins, stonefly nymphs were most abundant in unembedded-cobble substrata followed by 50% and 100% cobble-embedded conditions (Fig. 2B). Nymphs were most often found on the undersides of unembedded cobbles and on the sides of 50%-embedded cobbles. As with sculpins, when substrate effects were discounted, stoneflies did not distribute themselves differentially within any particular section in the channel. At the conclusion of the experiment, nearly all (99%) stonefly nymphs introduced were recovered alive.

Predator and Prey—Interactive

When placed together, sculpins and stoneflies were distributed similarly, in proportionate numbers, among three cobble-embeddedness conditions as when tested separately (Table 1). Greatest densities of sculpins and stoneflies were in the unembedded-cobble sections (Fig. 3A, B).

Stonefly numbers were 35, 20, and 15% lower, respectively, than numbers recorded from unembedded, 50%, and 100% cobble-embedded sections without predators. Although stonefly densities were altered by predation, numbers of stoneflies occupying the unembedded-cobble substrata were more than double those found in the cobble-embedded sections during the tests conducted without predators. Furthermore, mean stonefly numbers from the 50%- and 100%-embedded substrata were nearly identical between the two experiments.

DISCUSSION

Unembedded-cobble substrata supported the highest densities of sculpins and stoneflies when tested both independently and interactively. We propose that spatial refugia afforded

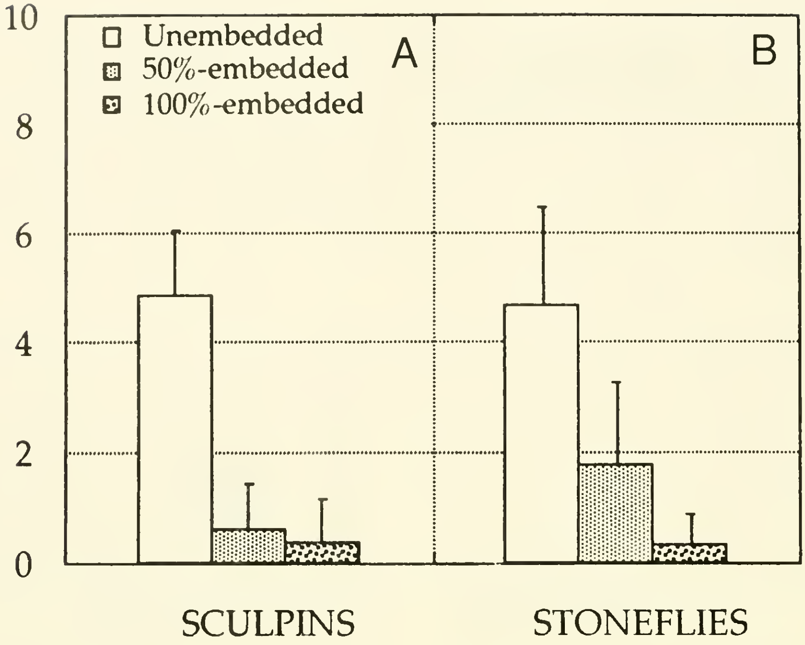

Fig. 3. Mean numbers of (A) *Cottus beldingi* and (B) *Skwala americana* recovered from three cobble-embeddedness conditions (n = 24) when tested interactively in streams. Vertical lines indicate 1 SD.

by the unembedded-cobble substrata influenced the distribution of *S. americana* more than the presence of vertebrate predators occupying mutually similar habitats. We submit that if the probability of prey escapement increases in unembedded cobbles because of expeditious access to refugia, then the stonefly may tolerate a greater risk of predatory attack. In theory, habitat-specific escape behavior can reinforce a prey's preference for habitats shared by coevolved predators (Lima 1992). According to Peckarsky (1982), prey that are smaller than their predators can effectively occupy interstitial spaces not habitable by predators. This hypothesis is supported by the fact that significantly more stoneflies occupied the 50%- than 100%-embedded cobble substrata, whereas sculpin densities found within these embedded substrata were nearly identical. Further, Davis and Warren (1965) found that, in a laboratory channel similar to one used in this study, prey consumption by *Cottus perplexus* significantly decreased as *Cottus* densities increased. High densities of *C. beldingi* in the unembedded-cobble substrata may have produced a similar interference response, thereby reducing the potential predation pressure on *S. americana*.

Predators have been shown to have nonlethal effects on prey by altering prey distribution (Power and Matthews 1983, Sih 1987, Kohler and McPeek 1989). However, results from our study generally do not support this type of response to predation. Our findings more closely approximate those of Sih et al. (1992), who reported that relative changes in prey density were attributed almost entirely to predation rather than predation-induced emigration.

While we did not conduct stomach analysis on the sculpin predator to confirm prey consumption in this study, earlier studies by Johnson (1985) in Lapwai Creek reported extensive predation of *S. americana* by *C. beldingi*. Accordingly, we surmised that reduced densities of prey at the conclusion of an experiment having sculpins present were due to predation alone.

In the field unembedded-cobble substrata likely offer better foraging conditions for *S. americana*, offsetting potential risks of sculpin predation. Siltation in riffle habitats reduces macroinvertebrate prey densities, especially mayflies (McClelland and Brusven 1980, Lenat et al. 1981, Peckarsky 1984), and may lower stonefly residence time within cobble-embedded patches. Short and Ward (1980) noted that low densities of S. *americana* in a Colorado mountain stream were not the result of limited food, but of siltation from bank erosion that reduced suitable habitat.

Macroinvertebrate densities from Lapwai Creek were much lower when the cobbles were 50–75% embedded than 0–25% embedded (Haro 1988). However, differences in macroinvertebrate abundance were not so great as to suggest prey was limiting to sculpins in these cobble-embedded substrata.

In conclusion, unembedded-cobble substrata in artificial streams provided spatial refugia for macroinvertebrates from sculpin predation. Stoneflies continued to select this microhabitat even though it harbored potentially dangerous sculpin predators. Cobble substrata can be greatly altered in sediment-laden, midorder streams draining agricultural lands (Haro 1988). Cobble impaction resulting in habitat degradation may destabilize ecological relationships between organisms that have coevolved in relatively silt-free and unembedded-cobble riffles. The importance of substrate condition in mediating predator-prey interactions in streams is becoming more evident (Feltmate and Williams 1989, Gilliam et al. 1989, Fuller and Rand 1990). Thus, the mechanisms by which and the extent to which nonpoint source sediment perturbations alter lotic food-web dynamics warrant careful consideration when evaluating stream ecosystems in the future.

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PERSISTENT POLLEN AS A TRACER FOR HIBERNATING BUTTERFLIES: THE CASE OF *HESPERIA JUBA* (LEPIDOPTERA: HESPERIIDAE)

Amy E. Berkhousen[1,2] and Arthur M. Shapiro[1,3]

Abstract.—Pollen grains of plants with well-defined flowering seasons may persist on insects through episodes of dormancy, such as hibernation. When readily recognizable and possibly confounding taxa can be excluded, these pollen grains can serve as direct evidence of life-history phenomena that are notoriously difficult to verify in the field. Pollen of the autumn-flowering composite *Chrysothamnus nauseosus* was used to demonstrate that the common montane skipper, *Hesperia juba*, hibernates as an adult in the Sierra Nevada. This is the first demonstration of adult overwintering in a temperate-zone hesperiid and may represent the smallest butterfly known to overwinter in a cold climate.

Key words: pollen carryover, hibernation, phenology, body size, Hesperia juba, Chrysothamnus nauseosus, Nymphalis antiopa.

Many life-history phenomena of insects, including seasonal dormancy and migration, can be inferred from phenological data but are notoriously difficult to demonstrate directly in the field; the animals are too few and/or difficult to find. Many Holarctic nymphaline butterflies have been suspected of hibernation since the 18th century, but there is still no direct evidence in many of them. Direct evidence requires either the post-hibernation recovery of individuals marked the previous season (or otherwise identifiable), or the discovery of hibernating individuals and the demonstration that they are able to survive winter in situ and enter the reproductive pool in spring. Despite the rarity of such evidence, the hypothesis of adult hibernation is repeated uncritically in most modern accounts of nymphaline biology. It is much more difficult to persuade anyone that a butterfly belonging to a lineage hitherto unsuspected of hibernation in fact overwinters as an adult.

Kettlewell (1961) and Kettlewell and Heard (1961) were able to use a radioactive particle originating from an atmospheric nuclear test in the Sahara Desert to trace the origin of a migrant moth (*Nomophila noctuella* Schiff., Pyralidae) collected in Britain. Pollen grains are a more prosaic surface contaminant of insect specimens which under favorable circumstances can serve the same purpose. Demonstration of even a single adherent grain of pollen of an autumn-flowering plant on a spring-collected insect could document the overwinter survival of that individual. There seems to be no prior documentation of such long-term pollen persistence. We applied the concept to the Californian skipper, *Hesperia juba* Scudder (Hesperiidae), which has been suspected of adult hibernation, using as our index pollen species the composite shrub *Chrysothamnus nauseosus* (Pall.) Britton, with encouraging results.

The difficulty of verifying hibernation is illustrated by Shapiro's previous studies of *H. juba* (Shapiro 1981). He marked 104 individuals at Donner Pass in the Sierra Nevada in September 1979. In June 1980 he captured 18 individuals in the same area, but none was marked. This was an unusually large-scale attempt at a direct demonstration of overwintering; hibernating nymphalids seldom occur at similar densities. Shapiro noted that the negative result was uninterpretable; the only meaningful result would have been the capture of one or more marked specimens.

NATURAL HISTORY OF *HESPERIA JUBA*

Hesperia juba is a common and widespread montane skipper in California and adjacent states. Despite its commonness, its life history remains very poorly known. MacNeill (1964) described the early stages based on laboratory

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rearing but did not understand its phenology. Misled by pooling data from a very heterogeneous mix of localities, he wrote that

> the adults are present from April through October, with some variation according to locality; evidently emergence is rather continuous and there are no distinct seasonal broods.

Emmel and Emmel (1973) recorded two distinct flights in southern California (April–June and August–September); and all subsequent local or regional data, from Oregon (Dornfeld 1980) to Baja California (Brown et al. 1992), have been similar. Shapiro (1979) was the first to point out that the phenology of *H. juba* was not only well defined but very unusual for a skipper. He presented eight years of Donner Pass data (1972–79) resulting from a biweekly sampling program. This study is now in its 21st year, and the pattern evident in 1979 has continued with great consistency (Table 1). *Hesperia juba* occurs at 5 of the 10 stations on Shapiro's northern California transect and is definitely resident at 4 of these; at all 4 it is spring/autumn bivoltine with slight variation in phenology, over an altitudinal range of 1500–2750 m.

No other hesperiine skipper is bivoltine at Donner Pass (2100 m) or higher, and no other skipper flies either so early in spring or so late in autumn. The only other bivoltine hesperiine in the region is *Polites sabuleti tecumseh* (Grinnell) at the lower limits of its range (1500 m on both the Sierran east and west slopes, but only irregularly bivoltine on the west). It is only about 60% the size of *H. juba*, but even so it emerges later in spring (much later at Donner Pass, where it is univoltine). At Donner, *H. juba* is often one of the first species to fly after snowmelt, along with the presumably adult-hibernating nymphalids and pupal-hibernating *Celastrina argiolus echo* (W.H. Edwards)(Lycaenidae) and *Pontia occidentalis* (Reakirt)(Pieridae). These and other circumstances described in Shapiro (1979) led to the suggestion that *H. juba* hibernates as an adult. Nonetheless, Scott (1986) ignored this suggestion, proposing instead that *H. juba* overwintered as a larva.

An overwintering larva would not be expected to feed and grow under a snowpack that normally persists for 6–7 months. Thus, growth would be limited to the periods of good weather between autumn flight and onset of snow, and between snowmelt and some (pupation) time before the spring flight—in all, a few weeks. Skippers grow slowly even under seemingly optimal conditions.

TABLE 1. Phenology of *Hesperia juba* at Donner Pass (2100 m) in the Sierra Nevada of California, based on roughly biweekly sampling, 1972–92.

Year	First flight	Second flight	N_1[a]	N_2[b]
1972	v.24–vi.7	viii.10–x.4	64	78
1973	not seen	ix.7–x.5	—	—
1974	vi.9	viii.24–ix.27	75	75
1975	vi.11	ix2.–ix.30	82	82
1976	v.14–vii.1	vii.20–x.8	49	96
1977	vi.4	ix.2–ix.23	90	90
1978	vi.14–vii.1	viii.15–x.23	45	61
1979	vi.1–vii.12	ix.4–ix.30	54	96
1980	vi.7–vii.5	ix.4–ix.27	61	89
1981	vi.7–vi.21	viii.6–ix.6[c]	36	50
1982	vi.23–vii.9	ix.1–ix.20	54	70
1983	vi.5–vii.12	viii.30–x.26	48	85
1984	v.27–vi.20	ix.6–ix.22	78	102
1985	v.23–vi.19	viii.20–x.5	63	90
1986	v.17–vi.15	ix.4	81	110
1987	vi.2	viii.11–ix.17	70	70
1988	iv.26–v.14	viii.19–ix.22	97	115
1989	v.20–vi.18	viii.28–x.8	72	101
1990	v.12–vi.2	ix.5–ix.18	95	116
1991	vi.2–vii.5	ix.4–x.12	61	94
1992	iv.28–vi.8	viii.22–ix.26	79	116

[a] Number of days from last observation of first flight to first observation of second flight.

[b] Number of days from first observation of first flight to first observation of second flight.

[c] No late-September sample taken (investigator out of country).

While attempting to carry various stages of *H. juba* overwinter in the laboratory, we reared a single larva from egg to (male) adult in 83 days at a continuous temperature of 26°C under outdoor photoperiod on growing *Poa* sp. (Gramineae). This individual developed without interruption (except for molts). We estimate the time available for circumhibernal larval development in an average year to be on the order of 75–85 days, nearly all with night temperatures below freezing and with afternoons reaching 20°C for perhaps 2–3 hr/day!

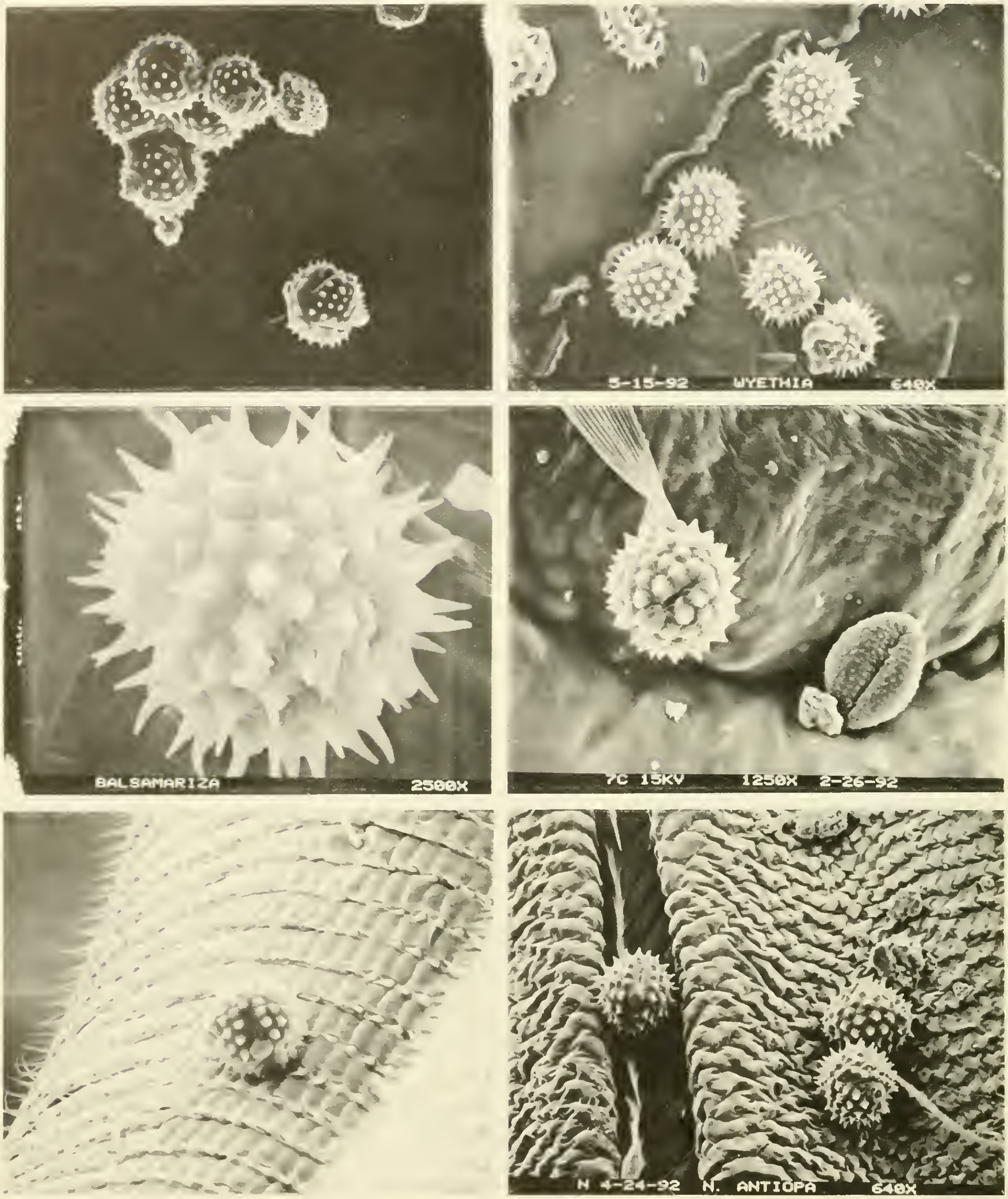
Most Holarctic *Hesperia* are univoltine (MacNeill 1964) although phenologically diverse even in a given location. In the northeastern United States, *H. metea* Scudder flies in early spring, *H. sassacus* Harris in late spring, *H. attalus* (W.H. Edwards) in summer, and *H. leonardus* Harris at the end of summer into autumn. In northern California there are distinctive populations of the *H. comma* L. complex that are univoltine from June to October in different localities (more than one species may be involved); *H. nevada* (Scudder) flies in early to midsummer at high elevation; *H. lindseyi* (Holland) is univoltine in late spring–early summer, slightly earlier than sympatric populations of the *comma* complex; only *H. columbia* (Scudder) is bivoltine, flying in foothill habitats in midspring (overlapping *H. lindseyi* a little) and again in early autumn (overlapping late "*comma*"). All Nearctic *Hesperia* appear to feed on perennial bunchgrasses, and all except *H. juba* have seasonal phenologies consistent with larval overwintering (albeit in different instars). One potential alternative explanation of the *H. juba* phenology, apparently falsified by this study, is that the nominal species *juba* consists of two wholly allochronic (spring and fall) univoltine populations, indistinguishable phenotypically. (A situation of this sort occurs in the *comma* complex on the western slopes of the Sierra Nevada, apparently involving sibling species that are, however, weakly phenotypically distinguishable.) The apparently universal sympatry of the putative populations argues against this hypothesis; if they were truly independent, surely there would be places where one occurs without the other.

The second flight of *H. juba* at Donner Pass coincides with peak flowering by the composite shrub rubber rabbitbrush, *Chrysothamnus nauseosus*. It and the polygonaceous subshrub *Eriogonum wrightii* Torr. ex Benth. (not visited by *juba*) are usually the only plants in flower at Donner then. *H. juba* visit this plant from midmorning until very late afternoon and are rarely seen anywhere else, or engaged in any activity but feeding. This contrasts with spring, when courtship, mating, and oviposition are all readily observed even though population densities are generally much lower. *Chrysothamnus* is visited by nearly all nectarivorous insects flying at that season, including the presumably hibernating nymphalids; late individuals of the larger fritillaries (genus *Speyeria*, Nymphalidae); the autumn-univoltine skipper *Ochlodes sylvanoides* (Bdv.); various lycaenid, pierid, and satyrid butterflies; bumblebees (*Bombus*) and honeybees (*Apis*) (Hymenoptera: Apidae); and many Diptera including Syrphidae, Bombyliidae, and Tachinidae.

Chrysothamnus is not a very prolific pollen producer, but we reasoned that its near monopoly on *H. juba* foraging in autumn and the near certainty that the last few feeding bouts prior to hibernation would have been on this plant make it an excellent candidate for persistent pollen detectable in spring.

METHODS

There seems to be only one published picture of *Chrysothamnus* pollen; its geographic origin is unspecified but likely is Utah (Solomon et al. 1973). We collected fresh pollen from *C. nauseosus* at Donner Pass in autumn 1991 (Fig. 1). We also collected fresh pollen from other composites whose pollen might cause confusion and which were in flower in spring 1992 at or near Donner Pass, whether or not they overlapped the first flight there. We obtained spring-collected specimens of *H. juba* from the Bohart Museum of Entomology, U.C. Davis (which has many from Donner Pass as vouchers of AMS's phenological and faunistic studies). We also collected spring 1992 specimens at Donner Pass. We did SEM searches for pollen following the methods of Courtney et al. (1982) with special attention to the facial cavity and basal portions of the proboscis. We did not attempt to identify non-composite pollens because we knew no non-composite whose phenology made it a potential indicator of overwintering.



Figs. 1–6. SEM studies: 1, *Chrysothamnus nauseosus*, Donner Pass, ix.1991, 640X; 2, *Wyethia mollis*, Donner, v.1992, 640X; 3, *Balsamorhiza sagittata*, Donner, v.1992, 2500X; 4, *Chrysothamnus* with another pollen, base of proboscis, *H. juba*, Donner, v.12.90, 1250X; 5, *Chrysothamnus*, proboscis, *H. juba*, Donner, vi.6.88, 1250X; 6, cf. *Chrysothamnus*, proboscis, *N. antiopa*, north Sacramento, v.1.88, 640X.

About 20 species of plants were in flower at Donner Pass during the 1992 spring flight; those visited by *H. juba* were *Phlox diffusa* Benth. (Polemoniaceae), *Calyptridium umbellatum* (Torr.) Greene (Portulacaceae), *Salix* sp. (Salicaceae), *Wyethia mollis* Gray, and *Taraxacum officinale* L. (Compositae). Of these, *Taraxacum* pollen is easily distinguished from *Chrysothamnus; Wyethia* is similar enough to require careful evaluation (see below).

RESULTS

At least 1 grain of *Chrysothamnus* pollen was found on 6/17 spring *H. juba* (Table 2), amounting to 25 of >374 grains examined (<7%). *Chrysothamnus* pollen was unevenly distributed among individuals: most grains were found on specimens bearing few pollen grains overall, and none or only one or two other pollen species. Specimens with heavy and diverse pollen loads tended to have no detectable *Chrysothamnus*. We interpret this as indicating that individuals just out of hibernation, which have had little chance to feed, are most likely to have carryover grains from the previous autumn. Subsequent feeding would either dislodge such grains or bury them in new pollen of other species, making them difficult to see. (Because fewer plants are in flower in early spring at the colder, drier east end of Donner Pass than in the west, spring specimens collected in the east are usually taken from bare soil and have very light or no detectable pollen loads in comparison to those from the west. Unfortunately, specimens taken before 1992 are merely labeled "Donner Pass.")

There are several composite genera presenting more or less similar spherical, tricolporate, echinate pollens that occur at or near Donner Pass. Several of these bloom at midsummer, in between the two flights of *H. juba*, and are not at issue. *Aster* and *Solidago* spp. often overlap the early part of the autumn flight. Since they never bloom in spring, any of their pollen found on *H. juba* would function as an indicator of hibernation. (Because they are so rarely still in bloom at the end of the flight, they are poor candidates for overwinter persistence. In fact, we have not detected them.)

TABLE 2. Occurrence of *Chrysothamnus* pollen grains on spring-collected *Hesperia juba* from Donner Pass.

Date of capture	Total pollen grains (all species)	*Chrysothamnus* pollen grains
vi.6.88	2	2
vi.6.88	0	0
v.12.90	10	10
v.12.90	10	0[a]
vi.1.90	10	10
v.8.92	15	1
v.8.92	>50	0
v.8.92	>100	0
v.8.92	7	0
v.8.92	2	0
v.8.92	4	0
v.8.92	2	1
v.8.92	10	0
v.8.92	20	0
v.8.92	7	0
v.16.92	25	1
v.16.92	>100	0
17	>374	25[a]

[a] One ambiguous grain on this v.12.90 specimen not counted as *Chrysothamnus*.

Pollens of the genera *Balsamorhiza* and *Wyethia* (both Heliantheae) are sufficiently similar to *Chrysothamnus* as to require careful diagnosis. *Balsamorhiza sagittata* (Pursh.) Nutt. occurs on andesitic ridgetops overlooking the pass. It is uncommon and in most years blooms during the second half of the first flight. *Wyethia mollis* is very abundant and widespread. It blooms slightly later, usually in the last third of the first flight. These pollens were found on spring *juba* but are easily distinguished from *Chrysothamnus* even at low magnification by their more acuminate and differently spaced echinae (Figs. 2, 3).

DISCUSSION

The concept of "pollen carryover" is familiar in pollination ecology (Handel 1983, Waser 1983), but there has been no incentive to look for truly long-term persistence. Wiklund et al. (1979) argued, based on studies of the wood white (*Leptidea sinapis* L. [Pieridae]), that butterflies are poor pollen vectors and that the lepidopteran proboscis is preadaptive for nectar "robbery." Flowers visited in Wiklund's study, however, were *Viola* (Violaceae) and *Lathyrus* (Leguminosae), which are normally pollinated by Hymenoptera and are neither "designed for" nor dependent on butterfly pollinators. Courtney et al. (1982) countered with data from several common Palearctic butterflies (including nymphalids reputed to hibernate), demonstrating not only significant pollen loads but relatively long pollen residence times (several days). From this they argued that butterflies, being relatively vagile, could be important agents of relatively long-distance pollination. Wiklund et al. (1982) countered that butterflies were still very inefficient as pollinators, and Tepedino (1983) noted that the usual, rapid decline in pollen viability with time would negate any dispersal advantage of butterflies as vectors. Venables and Barrows (1985) argued, based on studies of two North American species, that skippers did transfer pollen, but probably not very efficiently.

Chrysothamnus is visited by a great variety of insects and has a relatively generalized pollination syndrome. The relative efficiency of various visitors as pollinators is unknown, but seed set is typically heavy. Because the floral tube is long, the skipper must insert its proboscis deeply. The usual approach is from above, and many individuals dip forward far enough to bring the palpi and facial cavity into contact with the flower. We find occasional pollen grains on the legs and pelage as well as the mouthparts. Few approaches are made from the side, and it is unclear whether the proboscis could reach the nectar with this approach. We have observed *H. juba* using the forelegs to "groom" its head and antennae.

Tepedino's remarks on pollen viability are irrelevant to our study since, even if *Chrysothamnus* pollen remained viable overwinter, there would be no stigmas in spring to receive it.

We have found spherical, tricolporate, echinate, non-*Wyethia*, non-*Balsamorhiza* composite pollens on 5 of 8 presumably hibernated *Nymphalis antiopa* L. (Nymphalidae) selected haphazardly from the Bohart Museum's northern California series. As in *H. juba*, suspect pollen was most frequent on specimens bearing little pollen overall and few if any other species (Table 3). Some of these specimens are from low-elevation sites where *Chrysothamnus* does not grow, but other genera with similar pollens (*Aster, Solidago*, etc.) do. Shapiro (1986) argued, based on circumstantial, phenological evidence, that *N. antiopa* has a regular cycle of seasonal altitudinal migration in California. A more sophisticated study allowing us to discriminate among various summer- and autumn-flowering composite pollens west of the Sierra Nevada might permit a direct test of this hypothesis. Evidence in Table 3 is a credible, if not absolute, verification of the conventional wisdom that *N. antiopa* does indeed overwinter as an adult. It is inadequate to confirm migratory movement. (A European colleague has pointed out to us that *N. antiopa* reputedly does not visit flowers there. We have documented its visits to flowers in California by photograph as well as pollen studies.) Persistent pollen was used by Mikkola (1971) and Hendrix et al. (1987) to trace the sources of migrant Lepidoptera, including truly long-distance migrants.

There is a very remote possibility of secondary pollen transfer, i.e., that autumn pollens found on spring butterflies might have been acquired initially in autumn by other hibernating insects such as *Bombus* (Hymenoptera: Apidae) queens and redeposited in flowers where they were acquired by others. The abundance of grains in our study argues against this mechanism.

We have probably established that *Hesperia juba* overwinters as an adult, but not that

TABLE 3. Occurrence of *Chrysothamnus*-like pollen on spring-collected *Nymphalis antiopa* from high and low elevations in north central California. No attempt was made to discriminate among several *Chrysothamnus*-like pollens potentially available at low elevation, but all the genera bloom in late summer and autumn only. Note that the two vii.7.76 specimens from Sagehen Creek might be altitudinal immigrants from the late-spring emergence west of the Sierra (Shapiro 1986), while the vi.30.76 ones—based on phenotype and condition—probably overwintered locally.

Date and locality of capture		Total pollen grains (all spp.)	*Chrysothamnus*-like pollen grains
vi.30.1976	Sagehen Creek, Sierra County[a]	2	2
vi.30.1976	" "	7	7
vii.7.1976	" "	>150	0
vii.7.1976	" "	>100	0
iv.11.1977	Fairfield, Solano County[b]	13	6
iv.11.1977	" "	0	0
iv.13.1977	Willow Slough, Yolo County[b]	7	7
v.1.1988	North Sacramento, Sacramento County[b]	14	8
8		>293	30

[a] Elevation 1500 m; *Chrysothamnus* present.

[b] Elevation <100 m; *Chrysothamnus* absent.

this is its exclusive mode of overwintering. At lower elevations the time constraint on fall/spring larval development is less severe, and such a phenology becomes at least plausible. It would rarely be possible at Donner, but in rugged relief many microclimates occur, some of which might allow larval overwintering at least in some years. Some autumn females from Donner will lay fertile eggs, though they usually must be confined for at least a week before they do. Of 9 Donner females confined in autumn 1992, 3 laid a few fertile eggs and contained spermatophores; 2 contained mature or nearly mature eggs but no spermatophore; and 4 contained neither eggs nor a spermatophore at death. In 1992, 11 females were collected at Donner; of these 2 had mature eggs and none had spermatophores (Table 4). In addition, 3 were taken at Carson Pass, Alpine Co. (2700 m), 27 September 1992; of these 2 had neither eggs nor a spermatophore and the third had many eggs but no spermatophore. Interestingly, this last was being courted by a male when taken, the only courtship observed in autumn 1992. Perhaps females do not become attractive to males until they carry mature ova. Ford (1975) states categorically that nymphalids hibernate as virgins; clearly that need not be true for *H. juba*. (We attempted a small-scale experiment at carrying eggs overwinter 1991–92 at Donner, but all disappeared. We have also failed to carry third-instar larvae overwinter in refrigerators or freezers.) Spring females are almost always in breeding condition; 8 of 9 spring 1992 females dissected had both mature eggs and a spermatophore.

TABLE 4. Reproductive condition of 14 *H. juba* females collected in the Sierra Nevada in autumn 1992.

Date	Locality	Number of mature ova	Spermatophore present?
ix.2	Donner Pass	0	no
ix.2	"	0	no
ix.2	"	0	no
ix.18	"	0	no
ix.18	"	0	no
ix.18	"	3	no
ix.18	"	0	no
ix.18	"	13	no
ix.18	"	0	no
ix.18	"	0	no
ix.26	"	0	no
ix.27	Carson Pass	>25	no
ix.27	"	0	no
ix.27	"	0	no

H. juba is the largest hesperiine skipper in the Sierra and one of the two largest in California, but it is also the smallest butterfly known to hibernate as an adult in a climate with severe winters. A variety of relationships between body size and thermal biology has been postulated in Lepidoptera (Douglas 1986, Miller 1991). Naively, one might suppose that the heat-loss properties implied by surface/volume ratios might impose a lower limit of body size on butterfly hibernators. No hibernating insect can keep itself warm over winter by metabolic thermogenesis alone. Ability to hibernate must be related to the ability to get into a warm microclimate, lowering the freezing point by biochemical mechanisms, insulation, or some combination of these. Body size comes into play primarily in spring or autumn when the insect is active for part of the day but at risk for sudden, critical decrease of ambient temperature when the sun is obscured, or at dusk. A disadvantageous surface-to-volume ratio, uncompensated by insulation, could keep the insect from reaching shelter before it was immobilized by cold. We have watched nymphaline butterflies return to lava jumbles in late afternoon in the Sierra and quickly crawl to shelter, but we do not know where *H. juba* go.

Many insects much smaller than *H. juba* hibernate successfully in cold climates, but none is a butterfly. Those butterflies generally supposed to hibernate in the Holarctic (Nymphalidae: Nymphalini and Vanessini; Pieridae: *Gonepteryx* in the Palearctic and the Californian *Zerene eurydice* Bdv.) are remarkably uniform in size, though many butterflies of similar size do not hibernate. This is an interesting point, but we know too little of the energetics and physiology of butterfly hibernation to assess its significance. We merely note that *H. juba* is smaller than other known hibernators but is exceptionally large for a hesperiine skipper.

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BREEDING ECOLOGY OF LONG-BILLED CURLEWS AT GREAT SALT LAKE, UTAH

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ABSTRACT.—We quantified nest site characteristics, breeding densities, and migratory chronology of Long-billed Curlews at Great Salt Lake, Utah. The species is apparently declining in Utah, and little is know about their breeding ecology in the eastern Great Basin Desert. This study was designed to provide wildlife biologists with baseline data useful for their successful management. Curlews arrived in northern Utah in late March and generally departed by mid-August. Nest densities at Great Salt Lake ranged from 0.64 to 2.36 males/km^2. The habitat at curlew nest sites consisted of significantly shorter vegetation than nearby random locations ($\bar{x}$ = 5.7 versus 9.0 cm, respectively; $P < .01$). Nests tended to be located in small patches of vegetation near barren ground. Maintenance of relatively short vegetation appears to be important in managing curlew habitat. In addition, only 2 of 10 nests we monitored in 1992 were successful, with most lost to mammalian predators. Further research is needed to determine the impact of mammalian predators on curlew populations.

Key words: Long-billed Curlew, Numenius americanus, *nest site characteristics, migration chronology, Utah.*

Long-billed Curlews (*Numenius americanus*) historically were a common species in the grasslands of North America (Pampush 1980). Although quantitative population trend data are limited, it appears that habitat alterations and hunting dramatically reduced populations throughout their breeding range (Allen 1980, Pampush 1980). In Utah, Long-billed Curlews are presently being considered for listing as a sensitive species due to declining populations in the northern part of the state (Frank Howe, Utah Division of Wildlife Resources, Salt Lake City, personal communication). However, reasons for this decline are unknown. Therefore, wildlife managers in Utah require quantitative information on their breeding ecology in the eastern Great Basin Desert to successfully manage this species.

Two variables that wildlife biologists can manage to some extent are vegetation and predators. Previous studies in Idaho (Bicak et al. 1982, Redmond and Jenni 1986), Oregon (Pampush 1980), and Wyoming (Cochran and Anderson 1987) suggest that Long-billed Curlews select nest sites in grasslands with relatively short vegetation. Changes in vegetation height due to field fertilization, grazing, and precipitation can significantly affect curlew nest success (Bicak et al. 1982, Redmond and Jenni 1986, Cochran and Anderson 1987). In addition, predators can have a major impact on a curlew population because Long-billed Curlews initiate only one clutch per year and do not re-nest once a nest has been depredated (Redmond and Jenni 1986).

Little quantitative information has been published on the breeding ecology of Long-billed Curlews in Utah. Wolfe (1931) provided qualitative information on their habitat characteristics, and Forsythe (1972) described four nests found near Great Salt Lake. Our objective is to provide quantitative estimates of curlew migration chronology, current distribution and breeding densities, nest success, and nest site habitat characteristics at Great Salt Lake so that biologists managing this shorebird in northern Utah will have baseline information.

STUDY AREA

Our principal study areas were three state-owned wildlife refuges located along the eastern shores of Great Salt Lake (Paton and Edwards 1990): Howard Slough Waterfowl Management Area (WMA), 311 ha surveyed (41°10′N,112°10′E); West Layton marsh, 339 ha (41°0′N,112°0′E), and West Warren WMA,

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400 ha (41°20′N,112°05′E). Satellite study sites included North Ogden Bay WMA, 500 ha (41°15′N,112°10′E); Harold Crane WMA, 1300 ha (41°20′N,112°05′E); Locomotive Springs WMA, 1000 ha (41°40′N,112°55′); and northeast of Saltair Beach, 600 ha, (40°45′N,112°10′E). All sites receive approximately 25–38 cm of precipitation annually (Greer 1981) and are located at an elevation of 1283–1289 m. Marsh vegetation in these areas is dominated by bulrush (*Scirpus* spp.) and cattail (*Typha* spp.). Upland habitats are dominated by greasewood (*Sacrobatus vermiculatus*) and several species of Chenopodiaceae (*Salicornia europaea, Bassia hyssopifolia, Kochia scoparia, Suaeda calceoliformis*).

METHODS

Fieldwork was conducted 14 April–11 August 1990, 27 March–19 September 1991, and 19 March–10 September 1992. To determine curlew migratory chronology, distribution, and breeding densities, we surveyed principal study areas one day per week 1 April–31 August, except 1990, using spot-mapping techniques (Redmond et al. 1981). Surveys were started at sunrise and continued for 3–5 hours per day. Curlews were censused using only spot-mapping techniques at West Warren in 1992. Satellite study sites were visited 1–3 times per month all 3 years, with curlews counted from road transects during shorebird surveys (Paton et al. 1992). Weekly census data at Howard Slough and West Layton from 1991 and 1992 were compared using a paired *t* test.

To determine their breeding chronology in Utah, we actively searched for curlew nests in 1992 following methods outlined in Redmond (1986). Egg-laying dates for active clutches were determined using egg-floating techniques (Hays and LeCroy 1971). Observations of juveniles in 1990 and 1991 were used to supplement chronology data gathered in 1992. Clutch initiation dates for juveniles observed in the field were calculated by estimating age of the chick and then back-dating based on a 28-day incubation period (Redmond and Jenni 1986) and 6-day egg-laying period (Cochran and Anderson 1987).

We determined curlew nest site characteristics based on nests found in 1992. Vegetation was quantified using a line-intercept technique (Hays et al. 1981:40). To minimize the probability of attracting predators to active nests, measurements were made <1 week after nests either hatched or failed. Nest site habitat characteristics were quantified along four 15-m transects initiated at the rim of each nest scrape, with transects arranged in the four cardinal directions. To quantify the curlew habitat patch use patterns versus the available landscape, each nest had a paired set of transects, centered on a point located 50 m in a random direction (hereafter referred to as random sites). Random sites were located only in areas with potentially suitable habitat (i.e., dry, upland vegetation <15 cm tall; Pampush 1980, Redmond and Jenni 1986, Cochran and Anderson 1987). Vegetation height was measured at 0.5-m increments along the transect, starting at the nest rim (that is, 31 points per transect). The height of the tallest plant within 5 cm of the transect was measured. Plant species composition at nests and random sites was determined by measuring to the nearest 1 cm each plant species that touched the transect tape. For vegetation coverage analyses, we classified each 1-cm segment along transects as either live vegetation, dead vegetation, or barren ground.

We compared vegetation height at nests and the paired random sites with a paired *t* test to quantify vegetational differences between used and available patches. To quantify variation in vegetation height as a function of the distance from plot center, at both nests and random sites, we categorized the data into five 3-m-long distance segments. These distance segments were then compared using analysis of variance (ANOVA) and Duncan's Multiple Range Test to determine which segments differed using PROC ANOVA in SAS (SAS Institute 1988). Alpha values <.05 were considered statistically significant.

We compared ground coverage between nests and random sites using a paired *t* test for three vegetation categories (live, dead, and barren ground). To determine if the three vegetation categories differed as a function of the distance from plot center, we again classified the data into five 3-m-long segments. The distance segments were then compared using ANOVA and Duncan's test, at both nests and random sites.

TABLE 1. Maximum number of Long-Billed Curlews counted during weekly censuses at two study sites at Great Salt Lake.

	Howard Slough WMA			W. Layton WMA		
Date	1990	1991	1992	1990	1991	1992
Apr 1–7	NC[a]	5	4	NC	1	1
Apr 8–15	NC	13	6	NC	12	4
Apr 16–22	NC	8	10	NC	5	4
Apr 23–30	NC	12	7	NC	4	10
May 1–7	NC	9	14	NC	3	15
May 8–15	NC	6	12	NC	4	23
May 16–22	NC	5	14	NC	6	15
May 23–31	NC	9	11	NC	3	15
Jun 1–7	4	5	11	NC	5	14
Jun 8–15	0	3	4	2	5	9
Jun 16–22	1	0	2	2	3	3
Jun 23–30	0	1	6	3	6	3
Jul 1–7	0	2	3	3	9	5
Jul 8–15	1	1	10	1	2	10
Jul 16–22	0	0	10	3	5	8
Jul 23–31	0	0	20	1	8	5
Aug 1–7	0	0	0	0	4	8
Aug 8–15	0	0	1	0	1	3
Aug 16–22	0	0	0	0	0	0
Aug 23–31	1	0	0	0	0	0

[a] No census data

RESULTS

MIGRATION AND NESTING CHRONOLOGY.—Our weekly surveys were generally initiated 1 week after Long-billed Curlews started to arrive in Utah. Cursory surveys from mid- to late March and observations by Forsythe (1970) indicated that Long-billed Curlews arrive in Utah during the last week of March (Paton et al. 1992; Table 1). No curlews were observed at Howard Slough on 27 and 30 March 1991, while one bird was seen on 31 March. In 1992 no curlews were seen on visits to Howard Slough or West Layton on 19 March and Harold Crane on 26 March, whereas three birds were seen on 30 March at Howard Slough and two curlews were at West Layton on 31 March.

By mid-April most curlews that nested around Great Salt Lake appeared to have arrived and established territories. However, not all curlews seen during April were local breeding birds, as flocks of 2–20 birds were often seen flying north over the study sites during the second and third weeks of April. For example, a flock of 11 birds was migrating north on 11 April 1991 over Howard Slough. On 14 April, 20 curlews were foraging near Brigham City in a pasture not used by resident curlews. By the end of April all three years, flocks that appeared to be migrating curlews were no longer observed.

Long-billed Curlew nests were initiated from mid-April to mid-May in northern Utah, based on floating eggs and observations of juveniles. Analysis of egg-floating data from 1992 showed that four clutches were initiated in late April, three the first week of May, and three the second week of May. In addition, juveniles 3–4 days old were found on 23 May 1990 and 2 June 1990 at Locomotive Springs, and five broods (all >1 week old) were seen on the east side of Antelope Island on 23 May 1992. Based on back-dating, their nests were all started about the third to fourth week of April.

Fall migration was relatively early for most curlews at Great Salt Lake compared with other shorebirds (Paton et al. 1992). The number of curlews seen on our two principal study sites declined dramatically after the first week of June. We saw no obvious evidence to suggest that Long-billed Curlews attempted to re-nest after nests were depredated. In fact, most adults remained on territory for only 2–3 weeks after nests were depredated and then vacated the study areas.

There was an influx of birds at West Layton and Howard Slough from mid-July to late July (Table 1). These flocks were probably migrants, either from other areas around Great Salt Lake or possibly farther north. These flocks often had one or two adults (both sexes) and 2–4 juveniles, suggesting the possibility they were sometimes migrating family groups, although this has not been previously reported. The largest late-summer migratory flock we observed during 3 years of fieldwork was 38 birds on 25 July 1990 at Salt Well Flats, located at the northwestern corner of Promontory Point. It was extremely rare to see any curlews during surveys at our study areas after 15 August (Table 1). Our latest Utah record was one bird on 27 August at Layton.

DENSITY ESTIMATES.—In 1990, surveys were initiated too late to estimate the number of breeding adults at the principal study areas. Survey data from the two principal study areas suggested more curlews were sighted in 1992 than in 1991 (Howard Slough: $t = -2.51$, df = 19, $P < .02$; Layton: $t = -2.4$, df = 19, $P < .03$; Table 1). Howard Slough had 2 nesting pairs of curlew in 1991 (0.64 pairs/km^2) and 6 pairs in 1992 (1.92 pairs/km^2), while West Layton had 2 nesting pairs in 1991 (0.59 pairs/ km^2) and 8 pairs in 1992 (2.36 pairs/km^2). At West Warren, we estimated 9 breeding pairs in 1992 (2.25 pairs/km^2). Although the data are limited, nearest-neighbor nest distances averaged 480.4 m (range = 351–1158 m, $n = 6$).

Surveys at satellite study areas found no evidence to suggest that Long-billed Curlews nested at Harold Crane or north of Saltair during any year of the study. No curlews nested at North Ogden Bay in either 1990 or 1991, and 1–2 pairs nested there in 1992. Locomotive Springs was surveyed most thoroughly in 1990, when we estimated a minimum of 6 pairs nesting in the area. One of the largest nesting concentrations of curlews we observed at Great Salt Lake was in late May 1992 on the east side of Antelope Island, where at least 8 pairs were seen along 2 km of road approximately 1.5 km northwest of Seagull Point. Interestingly, other ground-nesting species (Short-eared Owls [*Asio flammeus*] and Northern Harriers [*Circus cyaneus*]) were also relatively common on the east side of Antelope Island, compared to other areas at Great Salt Lake (P. Paton personal observation).

CLUTCH SIZE AND NEST SUCCESS.—All nests in which we were able to determine final clutch size had four eggs ($n = 9$). Only 2 of the 10 nests we found in 1992 were successful. Seven nests were depredated by mammalian predators. Red fox (*Vulpes vulpes*) was the primary nest predator for Snowy Plovers on the east side of the lake (Paton and Edwards 1990) and probably depredated most curlew nests. In addition, one nest at Layton was possibly depredated by another curlew, based on the diameter of puncture holes found in the egg shells (Redmond and Jenni 1986). We were unable to determine fledging success.

NEST SITE CHARACTERISTICS.—Ten Long-billed Curlew nests were found in 1992. Curlews appeared to select nest sites in habitats with relatively short vegetation, often near barren patches of ground. Vegetation within 15 m of nest sites was significantly shorter than vegetation at random sites (paired $t = -10.7$, df = 1239, $P < .0001$; Table 2). Vegetation near nest sites (<6 m) was significantly taller than that far (≥ 6) from nests (Table 2). In contrast, there was no significant variation in vegetation height at random sites as a function of distance from plot center (Table 2).

Curlews selected nest sites in small clumps of live/dead vegetation, and near the nest there was relatively little barren ground (Table 3). In fact, the amount of barren ground near nest sites was the only vegetation variable that showed any significant variation as a function of distance from plot center (Table 3). Therefore, it appears that Long-billed Curlews did not select habitat patches based on the

TABLE 2. Mean (±SE) vegetation height (cm) of Long-Billed Curlew nest and random sites at Great Salt Lake, Utah ($n = 10$). Means lacking similar letters are significantly different (ANOVA, $P < .05$, Duncan's Multiple Range Test).

	Distance from plot center (m)							
	0–2.9	3.0–5.9	6.0–8.9	9.0–11.9	12.0–15.0	0–15.0	F	P
Nest sites	6.5 ± 0.3A	6.0 ± 0.4AB	5.3 ± 0.3B	4.9 ± 0.4B	5.5 ± 0.5B	5.6 ± 0.2	2.98	.018
Random sites	8.1 ± 0.5A	9.5 ± 0.8A	9.3 ± 0.8A	9.8 ± 0.7A	8.6 ± 0.7A	9.0 ± 0.3	1.11	.35

TABLE 3. Mean (±SE) vegetation coverage of Long-Billed Curlew nest and random sites at Great Salt Lake, Utah. Means lacking similar letters are significantly different (ANOVA, $P < .05$, Duncan's Multiple Range Test).

	Distance from plot center (m)							
	0–2.9	3.0–5.9	6.0–8.9	9.0–11.9	12.0–15.0	0–15.0	F	P
Nest sites								
% live vegetation	56 ± 4.6A	45 ± 5.6A	43 ± 6.1A	40 ± 6.3A	46 ± 6.6A	46 ± 4.2	1.1	.357
% dead vegetation	26 ± 4.2A	27 ± 5.9A	19 ± 5.4A	21 ± 5.7A	15 ± 4.5A	22 ± 4.3	1.0	.418
% barren ground	18 ± 3.9A	28 ± 5.2AB	38 ± 6.3B	39 ± 6.7B	39 ± 6.7B	32 ± 4.9	2.6	.037
Random sites								
% live vegetation	39 ± 6.3A	37 ± 6.0A	32 ± 5.5A	28 ± 5.9A	36 ± 6.4A	34 ± 4.6	0.5	.735
% dead vegetation	28 ± 6.1A	28 ± 5.6A	33 ± 6.9A	36 ± 6.9A	30 ± 6.2A	31 ± 5.2	0.3	.894
% barren ground	33 ± 6.4A	35 ± 6.7A	35 ± 6.7A	36 ± 6.4A	34 ± 6.6A	35 ± 5.9	0.1	.997

proportions of dead and live vegetation available, but rather vegetation height seemed to be the key variable. There was a weak tendency for curlew nest sites to be located in areas with slightly more live vegetation than in random transects ($t = 1.81$, df = 18, $P = .07$), whereas nests and random sites did not differ in the amount of dead vegetation ($t = -1.3$, df = 18, $P = .19$) or barren ground ($t = -0.3$, df = 18, $P = .74$; Table 3).

The most common plant species, with common defined as averaging >3% total coverage, within 15 m of the 10 nests were *Salicornia europaea* ($\bar{x}$ = 13.2% live, 7.7% dead), *Bassia hyssopifolia* (14.7% live, 3.2% dead), *Suaeda calceoliformis* (11.5% live, 6.1% dead), *Distichlis spicata* (4.3% live), and *Chenopodium album* (0.3% live, 3.2% dead).

DISCUSSION

Nesting densities in northern Utah found during this study were intermediate relative to estimates for other regions of western North America. Sadler and Maher (1976) reported relatively low densities (0.14–0.17 pairs per km^2) at the northern limits of their range in Saskatchewan, which would be expected. Densities similar to those in our study were found in southeastern Washington (0.58–1.45 pairs per km^2; Allen 1980) and north central Oregon (up to 3.6 per km^2; Pampush 1980), which would be expected given that both sites were at latitudes similar to those in northern Utah. An area with consistently high densities is the shortgrass rangelands of western Idaho (6.4 males and 5.3 females per km^2; Redmond et al. 1981). The exact reasons for this variation in population densities across the species' range are unclear, yet should be studied further to assess factors regulating their populations. For example, little is known about prey and predator densities in various parts of the curlew range.

Other aspects of Long-billed Curlew breeding ecology at Great Salt Lake were similar to results reported from other parts of their range. Four eggs is the typical clutch size for the species (Pampush 1980, Redmond 1986). Somewhat surprisingly, the migratory chronology of Utah birds was different from that of southeastern Washington (Allen 1980), with birds in northern Utah arriving later and remaining longer. However, although southeastern Washington is farther north than Utah, it is also lower in elevation (ca. 225 m) and has a milder climate than Great Salt Lake, which probably explains why curlews arrive earlier in Washington. As with the migratory chronology, clutch initiation dates vary with climate. Clutches in northern Utah were started from mid-April to mid-May during our study, which was 2 weeks later than in western Idaho (Redmond 1986), southeastern Washington (Allen 1980), and north central Oregon (Pampush 1980). However, in central Wyoming, clutches were initiated 1–2 weeks later than at Great Salt Lake (Cochran and Anderson 1987).

Vegetation height seems to be one of the fundamental habitat characteristics used by Long-billed Curlews to select breeding areas. Curlews tend to nest in areas with vegetation <10 cm tall (Allen 1980, Pampush 1980, Bicak et al. 1982, Cochran and Anderson 1987, this study). Structural characteristics of their nesting habitat at Great Salt Lake are relatively similar to those in other regions of western North America, although specific plants were different. As in this study, Pampush

(1980) found that curlews in north central Oregon selected nest sites with generally lower vertical profile and lower vertical density than the surrounding habitat. Bicak et al. (1982) found a negative correlation between Long-billed Curlew abundance and vegetation height, with more birds using areas with short vegetation. Since curlews use areas with relatively short vegetation, Bicak et al. (1982) suggested that livestock grazing prior to the onset of the breeding season could increase use of an area by nesting curlews. Redmond (1986) reported that relatively tall vegetation (40 cm tall) affected their foraging activities, and that an increase in plant height in nesting habitat (>12 cm tall) due to the previous year's growth delayed egg laying the subsequent year. Therefore, all studies in western North America indicate that relatively short vegetation is among the key habitat variables that wildlife managers must be concerned with to maintain curlew nesting habitat.

Nesting Long-billed Curlews at Great Salt Lake seem to prefer areas that provide good visibility of the surrounding habitat during incubation. This conclusion was similar to habitat studies from other parts of its range (Allen 1980, Cochran and Anderson 1987). At Great Salt Lake the ground is relatively level and curlews prefer to nest near the edges of barren alkali flats. Wolfe (1931) also reported that curlews nested near barren areas at Great Salt Lake. Interestingly, Cochran and Anderson (1987) reported that Long-billed Curlews avoided fields with extensive barren ground, although they did not determine if curlews had a threshold value for barren ground. Again, these data suggest that relatively short vegetation is preferred by nesting curlews.

Finally, more must be learned about the impact of nest predators on curlew populations in western North America. Red fox were first sighted at Great Salt Lake in the late 1960s, with fox numbers dramatically increasing during the recent Great Salt Lake flood years (1983–90; Val Bachman, Ogden Bay WMA, personal communication). Currently, red fox are commonly sighted on the eastern shores of Great Salt Lake (personal observation), whereas during 3 years of fieldwork on the eastern shores of the lake, we sighted only one coyote (*Canus latrans*) on one occasion. Interestingly, one area at Great Salt Lake where Long-billed Curlews are still relatively common, Antelope Island, also has coyotes. The interaction between coyotes and red fox requires further study. Impacts of nest predators on Long-billed Curlew populations could be devastating because Long-billed Curlews apparently do not re-nest after their eggs are depredated (Redmond and Jenni 1986). Therefore, additional work may be required of wildlife management to minimize depredation rates and thus maintain curlew populations in certain parts of their range.

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HABITAT USE AND BEHAVIOR OF MALE MOUNTAIN SHEEP IN FORAGING ASSOCIATIONS WITH WILD HORSES

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Key words: mountain sheep, Ovis c. canadensis, *wild horses, habitat use, behavior, Bighorn Canyon National Recreation Area, Montana, Wyoming.*

Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) maximize survival by foraging in secure habitats that afford high visibility and have good interspersion of preferred forage plants with escape cover (Risenhoover and Bailey 1985). Good visibility and precipitous escape cover are structural habitat elements that provide mountain sheep with security from predators (Buechner 1960, Geist 1971, Wishart 1978, Risenhoover and Bailey 1985).

Wild horses (*Equus caballus*) also maximize survival by foraging in secure habitats with good interspersion of preferred forage plants. However, different structural elements of the habitat provide security for mountain sheep and horses; mountain sheep select foraging areas near precipitous escape terrain while horses select foraging areas near open, flat terrain. This is due to basic differences in predator escape tactics for the species: mountain sheep climb to avoid predation and horses run.

Although grasses dominate the diets of both horses and mountain sheep, each species' predator-avoidance strategy selects for structurally different habitats. However, when spatial distributions overlap, a competitive situation may occur, with mountain sheep being negatively impacted. In several instances such competition with feral equids has resulted in mountain sheep declines (McMichael 1964, Weaver 1973, Seegmiller and Ohmart 1981).

A growing body of literature supports the hypothesis that horses and other exotics may, in some respects, facilitate the foraging effectiveness of some native ungulate species either by habitat modification or increased protection from predators (Berger 1978, 1986, Festa-Bianchet 1991). The purpose of this note is to present unique observations which suggest that male mountain sheep may benefit from close foraging relationships with wild horses. Few data exist on resource competition between mountain sheep and feral horses (Berger 1986), and though not statistically quantifiable, these limited observations support Berger's (1986) hypotheses regarding forage facilitation of native species by exotics.

STUDY AREA AND METHODS

The study was conducted at Bighorn Canyon National Recreation Area (BICA), a 48,679-ha National Park Service unit that has as its focal point a 114-km-long reservoir in southeastern Montana and north central Wyoming. Mountain sheep recolonized BICA in 1975 because of dispersal of 4–6 animals from a nearby transplant. By 1986 the population had increased to over 60 animals (Coates and Schemnitz 1986).

Portions of BICA are federally designated as the Pryor Mountain Wild Horse Range (PMWHR). The 17,402-ha PMWHR supports approximately 120 wild horses and is located 80 km south of Billings, Montana (Bureau of Land Management 1984).

The area is characterized as a desert-shrub woodland (Lichvar et al. 1985), and dominants include a sparse overstory of curlleaf mountain mahogany (*Cercocarpus ledifolius* var. *intercedens*), Utah juniper (*Juniperus osteosperma*), sagebrush (*Artemisia* spp.), and greasewood (*Sarcobatus* spp.), with a poorly developed understory of bunchgrasses (Lichvar et al. 1985). Annual precipitation averages

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15–20 cm. Soils present include limestone and sandstone in the precipitous canyonland and dolomite in the nonprecipitous areas (Knight et al. 1987). Elevations vary from a mean pool level of 1109 m at the reservoir to 2682 m at East Pryor Mountain.

Gray limestone cliffs rise >250 m vertically from the lakeshore. Cliff faces, ledges, and eroded limestone soils (karst topography) provide abundant escape terrain for mountain sheep. Escape terrain predominates the entire study area, from East Pryor Mountain to the reservoir. Other than an alluvial fan located at the northern extreme of the study area, virtually all habitat is within 300 m of cliffs, ledges, or karst topography (Coates 1988).

Three adult ewes (>18 months old) and a 6-year-old ram were captured and equipped with radio collars manufactured by Telonics (Mesa, Arizona). Systematic radio relocation of these animals provided the opportunity to locate and observe 328 groups of mountain sheep between June 1986 and November 1987.

Group size and age/sex composition were recorded for each observation. Additionally, three habitat parameters were analyzed: horse use (Yes/No), distance to precipitous terrain, and vegetation type. A preference ratio (percent use/percent availability) was used to analyze preference and/or avoidance of vegetation types (Risenhoover and Bailey 1985). Because escape terrain was nearly continuous throughout the southern portion of the study area (distance rarely >300 m), all habitat types were considered available to mountain sheep. The alluvial fan was considered available to mountain sheep, primarily to investigate differences in habitat selection between male and female cohorts of mountain sheep, and to analyze the influence of distance to escape terrain on foraging behavior.

The foraging behavior of adult mountain sheep was analyzed to determine the effects of habitat security on foraging efficiency (Risenhoover and Bailey 1985). Once a group of mountain sheep was located, a focal animal was selected for analysis of foraging behavior. Recognition of focal animals was aided by identifying marks on pelage or scars. Foraging behavior was observed for five consecutive 3-min periods to determine the amount of time the focal animal devoted to three behavioral categories: foraging, social, alert (Risenhoover and Bailey 1985). An animal was engaged in foraging when it actively ingested forage and when it moved about with animals that were actively ingesting forage.

An animal was engaged in social behavior for all intraspecific and interspecific interactions. Social interactions included looking at another animal, moving toward/away from another animal, and mother/young interactions. Alert behavior was recorded if the focal animal stopped foraging to look up in the typical alert posture for mountain sheep (i.e., ears up and neck outstretched; Geist 1971), if it looked at a disturbance (e.g., a vehicle on the highway, or a person approaching on foot), or when it ran to avoid a disturbance (e.g., a person approaching on foot). Foraging efficiency was calculated as percentage of time devoted to foraging behavior during the 15-min period. Percentage of time spent in alert or social interactions provided a measure of the relative security of mountain sheep in different habitats.

RESULTS AND DISCUSSION

Four vegetation types (Knight et al. 1987) occur within the observed range of mountain sheep: Utah juniper/mountain mahogany woodland (JU/CE), Utah juniper woodland (JUOS), mountain mahogany woodland (CELE), and Douglas fir woodland (PSME). Distribution of JUOS was limited to an alluvial fan at the north end of the study area and narrow fingers interspersed within the JU/CE habitat type. Horse use was always "No" for karst topography and "Yes" for the alluvial fan at the northern extreme of the study area, based on the presence/absence of horse feces observed during fieldwork. Horse use was also observed along fingers of nonprecipitous habitat interspersed throughout the JU/CE type. Distribution of PSME was restricted to a deeply incised drainage present in the core use area occupied by rams.

Overall, 85.7% of male mountain sheep observations involving mixed age/sex groups occurred in JU/CE woodland. JUOS, CELE, and PSME woodlands were used in 13.6, <1, and <1% of the observations, respectively (Table 1). The preference ratio for JU/CE is 4.5, indicating that mountain sheep foraging with conspecifics prefer this type (Risenhoover and

TABLE 1. Percent habitat utilization by male mountain sheep in foraging associations with conspecifics compared with associations with wild horses. Habitat preference ratios are expressed as + or – and are given in parentheses below each appropriate category.

	Habitat Type			
	JUOS	CELE	JU/CE	PSME
Male mountain sheep:				
With conspecifics	85.7	13.6	<1	<1
Habitat preference	(+)	(–)		
With wild horses	16.7	83.3	0	0
Habitat preference	(–)	(+)		

Bailey 1985). Preference for JU/CE habitat probably resulted more from the interspersion of escape terrain than from differences in visibility between habitats. Juniper was sparsely distributed throughout both JU/CE and JUOS types. Distinction between types was based on occurrence of curlleaf mountain mahogany rather than on increasing frequency of Utah juniper (Lichvar et al. 1985). Visibility obstruction was low in both JU/CE and JUOS habitats. Ewes never occupied the PSME type, even though it was located on rocky slopes, because visual obstruction was much higher than in JU/CE or JUOS.

Male mountain sheep were observed foraging with wild horses 22 times on 20 different days, and habitat parameters were recorded for 12 observations. Foraging associations usually involved 2 specific male horse/harem groups with bachelor ram groups. Ram group size ranged from 3 to 7 animals, 3 to 10 years of age. Female mountain sheep were never observed in association with wild horses. Horse group size was dynamic, but association usually involved 1 of 2 specific male horses accompanied by 5 to 8 mares and subadults. Of the 12 observations, 83.3% (n = 10) occurred in the JUOS vegetative type, and 16.7% (n = 2) occurred in JU/CE (Table 1). The preference ratio for JUOS is 1.2. The preference ratio for JUOS by male mountain sheep foraging with wild horses is noteworthy because habitat utilization patterns for JU/CE and JUOS were reversed when male mountain sheep associated with wild horses (Table 1).

These limited observations suggest that male mountain sheep foraging with conspecifics may prefer the JU/CE vegetation type, but male mountain sheep foraging with wild horses may prefer JUOS. Conversely, male mountain sheep foraging with conspecifics avoided JUOS, but male mountain sheep foraging with wild horses avoided JU/CE.

Grasses accounted for <1% of the vegetative cover in the JU/CE type but approximately 6% of the JUOS type (Knight et al. 1987). Although grasses were present in low composition in both vegetation types, mountain sheep foraging in JUOS had a higher availability of grasses.

Average distance to escape terrain was determined for male mountain sheep that foraged with conspecifics and compared to the distance for male mountain sheep that foraged with wild horses (Table 2). Male mountain sheep foraging with conspecifics remained within an average of 47 m (SD 69.5 m) from escape terrain, partially because of the ewes' reluctance to venture farther than 50 m from secure habitat. However, male mountain sheep foraging with wild horses were an average of 217 m (SD 310 m) from escape terrain. These limited data suggest that male mountain sheep foraged farther from escape terrain (in less secure habitat) when associated with wild horses than with conspecifics.

Foraging efficiency of mountain sheep with wild horses was 100% for all 12 locations (no alert or social interactions). Male mountain sheep that foraged with wild horses ignored disturbance (e.g., they could be approached readily, and they rarely looked up to scan their surroundings even when horses were fighting in their vicinity). Group size ranged from 9 to 16 animals, including rams and horses. Foraging efficiency of male mountain sheep with conspecifics was only 66% (n = 67) and was characterized by high levels of aggressive or social interaction (Table 3). Aggressive interactions were exhibited between rams when two or more followed a ewe, and when they established dominance rank in the male cohort. Social interactions between rams occurred when they attended ewes. Aggressive or social interactions were never observed when male mountain sheep foraged with wild horses. This may have been due to size-related dominance in mountain sheep (Geist 1971) and subordinate behavior of male mountain sheep in the presence of the relatively large wild horse (Berger 1986).

TABLE 2. Average distance to escape terrain (m) of male mountain sheep in association with conspecifics compared to distance when associated with wild horses. Standard deviations shown in parentheses.

	Distance to escape terrain (m)
Male mountain sheep:	
With conspecifics	47 (SD 69)
With wild horses	217 (SD 310)

TABLE 3. Average foraging efficiency of male mountain sheep in foraging associations with conspecifics compared with associations with wild horses.

	Percentage of time devoted to three activities while foraging		
	Foraging	Social	Alert
Male mountain sheep:			
With conspecifics	66	32	1
With wild horses	100	0	0

The subordinant/dominant relationship between male mountain sheep and wild horses was suggested both by the sheep's lack of aggressive behaviors while foraging and by the behavior of male wild horses directed toward male mountain sheep. Male wild horses were observed herding, or driving, male mountain sheep (n = 3) in a manner similar to the typical posture used when herding females (Feist 1975, Berger 1986). This typical herding posture consisted of running toward a female horse, or in this case a male mountain sheep, with ears flattened against the head, neck outstretched, and head held low to the ground.

Another indication of the subordinant/dominant relationship between mountain sheep and wild horses was extended penis behaviors that Feist (1975) described as a mechanism to establish dominance in wild horse groups. These extended penis behaviors were directed by a subordinant male wild horse (without harem) to a 9-year-old male mountain sheep with three other rams ages 3 to 7. There were no other horses in the vicinity. By exerting dominance over male mountain sheep or allowing rams to enter their harem, stallions can potentially elevate their own dominance rank and subsequent reproductive success by attracting additional females.

In summary, we believe that, contrary to some literature (McMichael 1964, Weaver 1973, Seegmiller and Ohmart 1981), male mountain sheep and wild horses can have beneficial relationships. Habitat selection by mountain sheep is a complex function of season, age, reproductive status, and sex of the animal (Smith 1992). This paper presents analyses suggesting that habitat selection and foraging efficiency may also be influenced by association with another species during foraging periods. These data support Berger's (1986) hypothesis that feral horses may perhaps serve either as competitor or as facilitator, depending on ecological conditions. In this case they served as competitor for a patchy supply of grasses, but possibly also as facilitator by increasing foraging efficiency in insecure habitat. Dominance rank of male horses may have increased as a result of the relationship. Sample sizes were small, but these unique observations suggest that male mountain sheep in association with wild horses foraged farther from escape terrain, enabling them to use areas that supported higher composition of grasses than areas used with conspecifics. Also, male mountain sheep did not exhibit aggressive behaviors while in association with wild horses and thus had higher foraging efficiency than those with conspecifics. To the best of our knowledge, foraging associations of this type have not been previously reported.

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FISH MORTALITY RESULTING FROM DELAYED EFFECTS OF FIRE IN THE GREATER YELLOWSTONE ECOSYSTEM

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Key words: fish kill, fire, suspended sediment, Greater Yellowstone Ecosystem, storm, debris torrent.

Often public concern focuses on the immediate, terrestrial impacts of wildfire. Such was the case during the summer and fall of 1988 when fires burned 562,000 ha in the Greater Yellowstone Ecosystem (GYE; Christensen et al. 1989, Schullery 1989). Besides the obvious loss of vegetation, less apparent, short-term consequences of these fires to terrestrial ecosystems included greater nutrient availability, widespread soil modification, and direct and indirect mortality of wildlife (Christensen et al. 1989, Singer et al. 1989). But as a result of the linkages between streams and their valleys (Hynes 1975), fires also may affect the hydrology, water chemistry, and geomorphology of aquatic ecosystems (Tiedemann et al. 1979, Schindler et al. 1980, Minshall et al. 1989). One consequence of fire is that bed- and suspended-sediment loads are often abnormally high in streams after storm events (Minshall and Brock 1991). Depending on the concentration and duration of exposure, suspended sediment can induce physiological stress, reduce growth, and cause direct mortality in fish (Newcombe and MacDonald 1991). However, as terrestrial vegetation recovers and soils stabilize, concentrations of suspended sediment in streams are expected to decline (Minshall et al. 1989). Unfortunately, little else is known about relations between watershed recovery and aquatic ecosystems following fire.

During the 1988 fires in the GYE, Minshall et al. (1989) observed fish kills in streams, but the extent and causes of mortality were not reported. While conducting other studies of watersheds in the GYE, we observed a fish kill in a burned watershed that occurred two years after the fires. In this paper we describe aspects of this fish kill and relate them to hydrologic conditions in this stream and those in a nearby stream with an unburned watershed.

STUDY AREA

We studied two tributaries of the North Fork Shoshone River in the North Absaroka Wilderness Area adjacent to the eastern border of Yellowstone National Park in the Absaroka Mountains of northwestern Wyoming. Jones Creek drains a 6423-ha watershed that was almost completely burned in 1988. Because of steep topography, drainage comprises numerous high-gradient tributaries and steep ephemeral chutes. The 4946-ha Crow Creek watershed is the next drainage south of Jones Creek watershed, has similar topographic relief and watershed orientation, and still supports extensive mixed-age stands of conifers. Both watersheds consist of geologically young and highly erodible volcanic soils (Minshall and Brock 1991).

METHODS

On 17 and 18 August 1990 we surveyed 1774 m of the stream channel and lower and upper banks of Jones Creek for dead fish following storm flows that had been caused by rain that began at 1600 hours on 16 August. Fish were identified, measured, and examined to determine possible causes of death. We examined the external anatomy of the fish, including skin, eyes, and gills, as well as stomachs of several fish.

Suspended sediment and discharge data from April to September 1990 were obtained from continuous remote sampling stations operated by the U.S. Geological Survey (USGS 1990). Suspended sediment concentrations are daily means based on 2–4 samples per day; mean daily discharge was based on hourly observations. On 17 August we collected two grab samples from Jones Creek to quantitatively assess the unusually high concentration of suspended sediment observed during the storm. Samples were collected at mid-depth in 0.5 m of water. We analyzed the grab samples for total suspended sediment by filtering them through Whatman grade 934AH fiberglass filters (1.5 μm effective pore size), oven-drying them for 1 week to constant weight, and then measuring them and averaging the results to determine the total concentration of suspended sediment (APHA 1989).

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RESULTS AND DISCUSSION

On 17 and 18 August 1990, 1 rainbow trout (*Oncorhynchus mykiss*), 4 Yellowstone cutthroat trout (*O. clarki bouvieri*), 11 brook trout (*Salvelinus fontinalis*), and 2 Yellowstone cutthroat trout × rainbow trout hybrids, all ranging from 190 to 410 mm total length, were found dead during surveys of Jones Creek. We found fish only in or near obstructions to flow (e.g., debris accumulations and boulders); thus, our survey probably overlooked dead fish that had been transported downstream or buried in newly formed bars. We believe that fish collected on 17 August had died recently because rigor mortis had not set in. Fish collected the following day were rigid and had started to dry; we suspect these also had succumbed on 17 August. Surveys on seven other occasions on Jones Creek (including 16 August) and eight other occasions on Crow Creek failed to reveal any moribund fish.

Each fish we examined appeared to have been asphyxiated by sediment. Typically, sediment completely embedded the gills of each fish, and individual lamellae often were difficult to see (cf. Cordone and Kelley 1961: 192). Eyes and skin appeared to be relatively normal, and fish lacked contusions and lacerations. Stomachs we examined appeared normal, and all contained recently consumed invertebrates.

Timing of the fish kill coincided with storms that began on 16 August and continued into the early morning of 17 August. Nearly 2.3 cm of rain was recorded on 16 August, followed by an additional 0.7 cm the next day. Though discharge in Jones Creek peaked on 16 August, concentration of suspended sediment did not appear to peak until 17 August (Fig. 1). And though suspended sediment concentrations on 17 August were the highest recorded from April to September 1990 (USGS 1990), concentration of suspended sediment in grab samples (9680 mg/L) was more than an order of magnitude higher than the daily mean concentration (587 mg/L) recorded for that date. Because the continuous remote sampling station collects samples at intervals, it is likely that the automated sampling missed the instantaneous peak concentration of suspended sediment. Likewise, it also is possible that our grab samples did not represent the instantaneous peak concentration.

Suspended sediment is known to be lethal to salmonids, but usually at higher concentrations and/or for longer exposures (Redding et al. 1987, Newcombe and MacDonald 1991) than we observed in Jones Creek. For example, Newcomb and Flagg (1983) calculated that a 36-h exposure to a suspended sediment concentration of 9400 mg/L would kill 50% of juvenile chinook salmon (*O. tshawytscha*) and sockeye salmon (*O. nerka*). However, lethal effects of suspended sediment may be more pronounced in the field than in the laboratory. In live-box tests in streams affected by ashfall from Mount St. Helens, concentrations of suspended sediment as low as 488 mg/L killed 50% of chinook salmon smolts after a 96-h exposure (Stober et al. 1981). But in comparable laboratory tests, a concentration of 19,364 mg/L was required to produce the same mortality rate (Stober et al. 1981). Clearly, suspended sediment concentrations in Jones Creek were stressful for trout. For the 24 h beginning at 1600 on 16 August, we estimated a minimum stress index of 11.3 $\text{mg}\cdot\text{h}\cdot\text{L}^{-1}$ (Newcombe and MacDonald 1991), which is near the value associated with lethality in adult salmonids (12 $\text{mg}\cdot\text{h}\cdot\text{L}^{-1}$; C. P. Newcombe personal communication).

Other factors may have contributed to the fish kill in Jones Creek. Newcombe and MacDonald (1991) and C. P. Newcombe (personal communication) suggested that high or fluctuating temperatures may increase the sensitivity

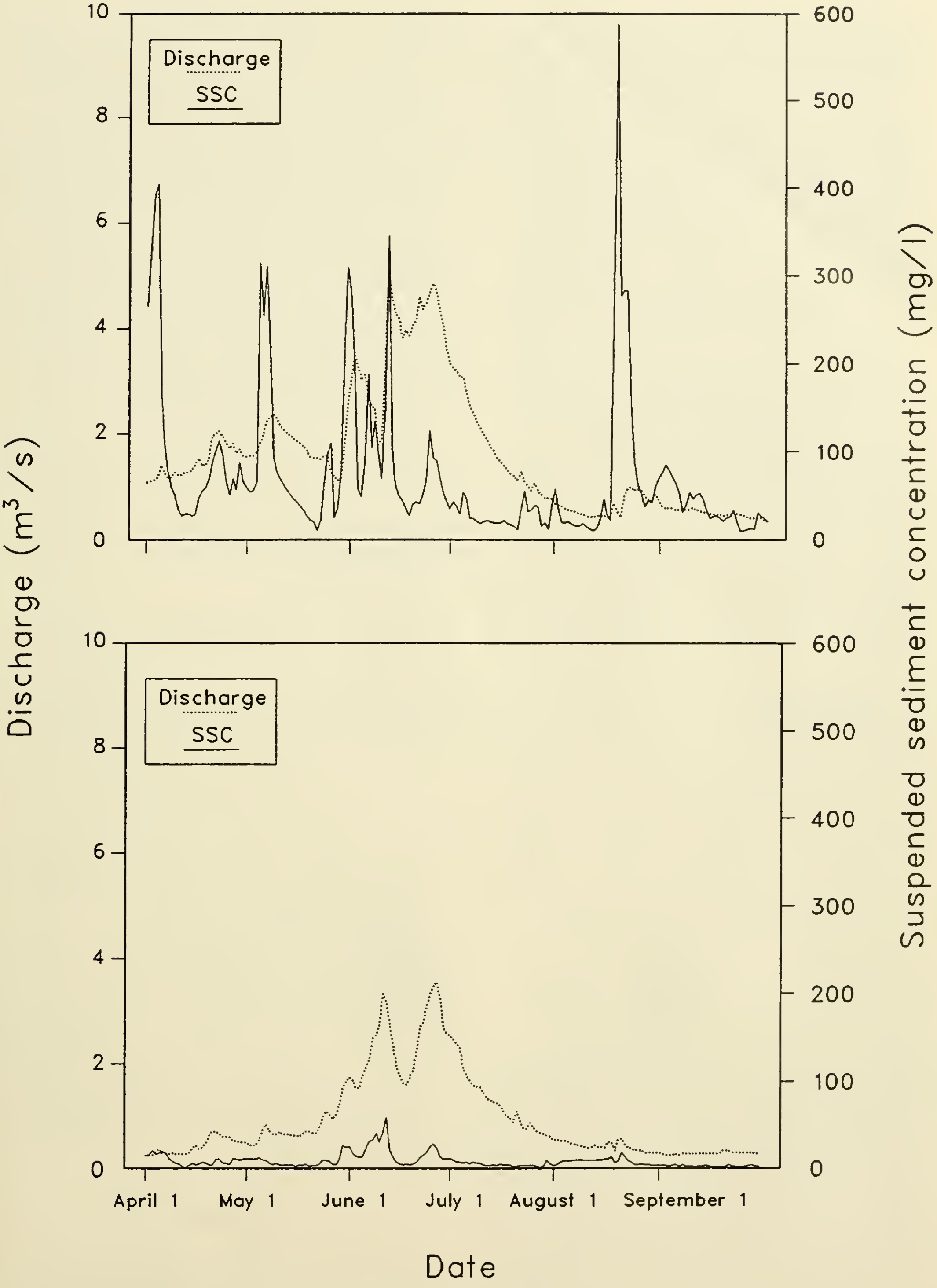

Fig. 1. Discharge and suspended sediment concentrations from April through September 1989 in Jones Creek (above) and Crow Creek (below), Wyoming (USGS 1990). The peak in suspended sediment in Jones Creek on 17 August coincides with the fish kill.

of trout to suspended sediment. In Jones Creek, water temperature varied from 10.1 to 17.3°C on 17 August (USGS 1990), but this fluctuation was equaled or exceeded on 70 of the 137 monitored days. Furthermore, these temperatures are largely within the range of those reported from other tests (e.g., Newcomb and Flagg 1983, 15–17°C; Redding et al. 1987, 12.5–13.5°C). A reduction in dissolved oxygen concurrent with peak suspended sediment concentrations, or other changes in water chemistry, may also have contributed to mortality, but we did not measure these parameters.

Tiedemann et al. (1979) indicated that landslide activity in steep drainages increases after wildfires. In Jones Creek a debris torrent down a tributary, apparently caused by heavy rainfall on unstable burned slopes, may have produced the high concentrations of suspended sediment on 17 August. After surveying farther upstream on subsequent days, we found a fresh debris and mud jam in Jones Creek near the mouth of a severely eroded tributary. Possibly because the stream was downcutting through this material, concentrations of suspended sediment remained high for several days (Fig. 1). Once activated by rainfall, numerous other ephemeral channels also carried silt-laden water for several days, but in concentrations visibly less than the peak concentration observed in Jones Creek.

The effects of fires on streams include increases in discharge and suspended sediment (Tiedemann et al. 1979, Schindler et al. 1980), and these differences seem evident in the comparison between the burned Jones Creek and the unburned Crow Creek watersheds. Discharge and suspended solid concentrations in Jones Creek were relatively high and erratic throughout the 137-day sampling period (Fig. 1). During this time the daily mean concentration of suspended sediment averaged 73.9 mg/L (USGS 1990). Though concentrations of total suspended sediment often increased with stream discharge (e.g., during spring runoff), pronounced episodic peaks in the concentration of suspended sediment also occurred during lower discharges, apparently associated with summer rainfall (e.g., as seen 16–21 August).

In contrast, discharge and suspended solid concentrations in the unburned Crow Creek watershed were markedly lower and more stable (Fig. 1). As in Jones Creek, suspended sediment increased during snowmelt and storm events, but changes appeared more proportional to increases in discharge. Daily mean concentrations of suspended sediment averaged 8.2 mg/L; the maximum daily mean concentration recorded (59 mg/L) was less than the Jones Creek average for the entire sampling period. Unfortunately, though the contrast between responses of both watersheds was quite marked, the lack of pre-fire hydrologic data makes it difficult to conclude that this contrast was the result of fire. However, during observations made on both streams for 4 weeks over 2 years, we did not witness similar concentrations of suspended sediment or a fish kill in either stream. At least circumstantially, the fish kill appears to be related to the unusually large hydrologic event associated with a rainstorm in the Jones Creek watershed.

The fish kill that we observed was notable because it occurred 2 years after the fire and appeared to result from an acute exposure to sediment. The extent and frequency of lethally acute concentrations of suspended sediment, as well as their effect on entire fish populations, are unknown. Previous fires in the Yellowstone area in the 1700s were at least as intense as those that occurred in 1988 (Romme and Despain 1989) and may also have produced slope instability, high suspended sediment concentrations, and, consequently, fish kills. In both Jones and Crow creeks we found remnants of the toes of landslides and the termini of debris flows that may have resulted from past fires. Because fire is a natural disturbance that will recur, further investigations are needed to gain a better understanding of the effects of fire and how watersheds, streams, and fish populations respond immediately and during the successional recovery of adjacent terrestrial vegetation.

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COLONY ISOLATION AND ISOZYME VARIABILITY OF THE WESTERN SEEP FRITILLARY, *SPEYERIA NOKOMIS APACHEANA* (NYMPHALIDAE), IN THE WESTERN GREAT BASIN

Hugh B. Britten[1], Peter F. Brussard[1],
Dennis D. Murphy[1], and George T. Austin[2]

Abstract.—Thirteen *Speyeria nokomis apacheana* (Edwards) (Nymphalidae) populations from the western Great Basin were assayed for isozyme variability using starch-gel electrophoresis. Eight of the 25 presumptive isozyme loci analyzed were found to be polymorphic. Collections made in 1991 and 1992 allowed for between-year comparisons of heterozygosity and the estimation of effective population size for five of the sampled populations. *Speyeria nokomis apacheana* populations exhibit lower mean heterozygosity levels than other nymphalids. This may be attributed to genetic drift in apparently isolated populations with small effective sizes.

Key words: Lepidoptera, protein electrophoresis, population structure, heterozygosity, Great Basin, gene flow.

The western seep fritillary, *Speyeria nokomis apacheana* (W. H. Edwards) (Nymphalidae), is confined to mesic areas in the Great Basin where both its larval foodplant, *Viola nephrophylla* (Greene) (Violaceae), and the most important adult nectar source, *Cirsium* (Mill.) (Asteraceae), co-occur. Adults of the single brood are present from late July through mid-September and are rarely observed far from colony sites. Population sizes are variable. Some colonies contain many hundreds of individuals, while others can be quite small with fewer than 10 adults observed over several days.

Small, isolated populations theoretically are exposed to a number of demographic, environmental, and genetic threats to their persistence (Gilpin and Soulé 1986, Shaffer 1987, Boyce 1992). Long-term persistence of such populations usually requires dispersal among numbers of populations. In this way extirpated populations are recolonized, and declining populations are genetically and demographically augmented. Protein electrophoresis is a useful tool for assessing population structure and levels of genetic variability in species with this type of distribution (e.g., Vrijenhoek et al. 1985, Waller et al. 1987, Dinerstein and McCracken 1990). The two goals of this study were to ascertain population structure of *Speyeria nokomis apacheana* in the western Great Basin and to estimate levels of isozyme variability within its populations.

Materials and Methods

Speyeria nokomis apacheana adults were collected from 10 sites in Nevada and eastern California in late August and September 1991

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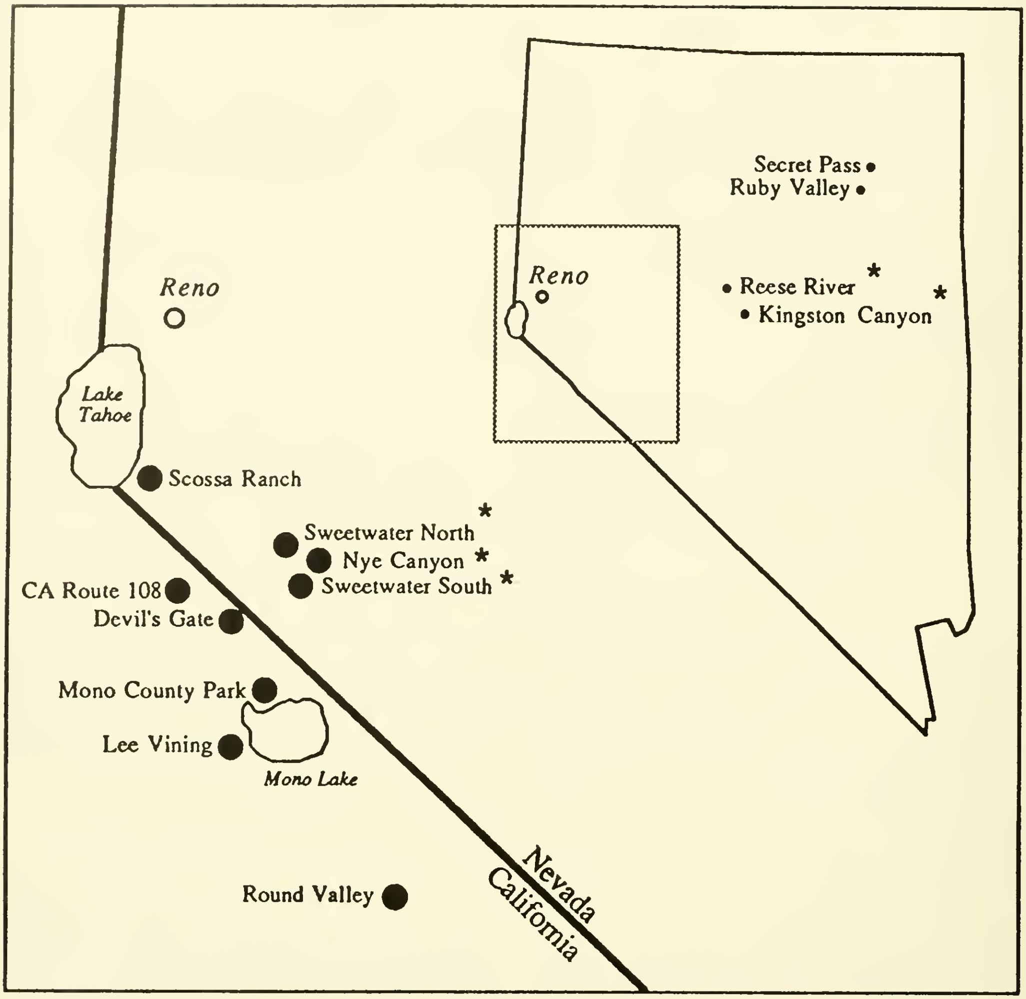
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Ruby Valley
Reno
Reese River
Kingston Canyon
Reno
Lake Tahoe
Scossa Ranch
Sweetwater North
Nye Canyon
Sweetwater South
CA Route 108
Devil's Gate
Mono County Park
Lee Vining
Mono Lake
Round Valley
Nevada
California

Fig. 1. Map of the western Great Basin with *Speyeria nokomis apacheana* collection sites denoted with closed circles (●). Sites sampled in 1991 and 1992 are indicated by *.

and from 8 sites in late summer 1992 (Fig. 1). One or two collectors sampled each population, and collecting efforts required 1–3 h per site. Captured individuals were frozen in liquid nitrogen for transport and were subsequently stored in an ultra-cold freezer at −80°C. Allozyme variation was assayed at 25 presumptive loci (Table 1); general methods and procedures followed Brussard et al. (1985).

Genotype frequencies were obtained by direct count from phenotypes observed on the gels. The most common electromorph (allozyme) at each locus was designated as "C," with relatively faster migrating allozymes scored as "B." Still faster migrating allozymes were scored as "A" alleles. Likewise, allozymes that migrated slower than the "C" alleles were designated as "D," and progressively later letters in the alphabet were assigned to still slower allozymes.

Data from each year of sampling were analyzed separately. Estimates of polymorphism level and heterozygosity and tests for conformance to Hardy-Weinberg expectations were made using BIOSYS-1 (Swofford and Selander 1981). A X^2 test for heterogeneity (Sokal and Rohlf 1981) was used to test the significance of allele frequency differences between populations at all polymorphic loci. Fixation indices (F-statistics) were estimated for a hierarchy with three levels: total sample, regional samples, and individual populations. Regions were delineated as (1) western, including nine sites in eastern California and

TABLE 1. Enzymes assayed and buffer systems used in the protein electrophoretic analysis of *Speyeria nokomis apacheana* populations in the Great Basin.

Locus	Enzyme	Enzyme commission number	Buffer
AAT-1,2,3	Aspartate aminotransferase	2.6.1.1	R[a]
AK	Adenylate kinase	2.7.4.3	4[b]
DIA	NADH diaphorase	1.8.1.4	R
GP-1,2,3	General (unidentified) protein		C[c]
GPI-1,2	Glucosephosphate isomerase	5.3.1.9	4
G6PDH	Glucose-6-phosphate dehydrogenase	1.1.1.49	4
HBDH	Hydroxybuteric dehydrogenase	1.1.1.30	R
IDDH	L-iditol dehydrogenase	1.1.1.14	R
IDH-1,2	Isocitrate dehydrogenase	1.1.1.42	C
MDH-1,2	NAD Malate dehydrogenase	1.1.1.37	4
MDHP	NADP Malate dehydrogenase	1.1.1.40	C
MPI	Mannosephosphate isomerase	5.3.1.8	R
PEP-A	Peptidase (glycyl-leucine)	3.4.-.-	R
PEP-E-1,2	Aminopeptidase (cytosol)	3.4.11.1	4
PGD	Phosphogluconate dehydrogenase	1.1.1.43	C
PGM	Phosphoglucomutase	5.4.2.2	R
SOD	Superoxide dismutase	1.15.1.1	C

[a] From Ridgeway et al. (1970).
[b] From Selander et al. (1971).
[c] Electrode buffer, 0.04 mol/dm^3 citric acid adjusted to pH 6.1 with *N*-(3-amino-propyl)-morpholine; diluted 1:10 for gel buffer (Clayton and Tretiak 1972).

western Nevada; (2) central, including Reese River and Kingston Canyon sites; and (3) eastern, including Secret Pass and Ruby Valley sites (Fig. 1). Because F-statistics are hierarchical "inbreeding coefficients" (Hartl and Clark 1989), they can be used to compare directly relative levels of gene flow among populations within regions and among populations within the total sample. The simultaneous test procedure (Sokal and Rohlf 1981) was used to test for homogeneity of genotype frequencies among samples in the western region to provide further insight into population structure along the eastern slope of the Sierra Nevada. The genetically effective number of migrants per generation (Nm) within homogeneous groups of populations was estimated from the F-statistics following Slatkin (1987). Samples from sites collected in both years were pooled for the calculation of genetic distances. The UPGMA clustering algorithm was used to derive a phenogram based on genetic distances.

Genetically effective population sizes (N_e's) were calculated for populations sampled in both 1991 and 1992 using the methods of Nei and Tajima (1981) and Pollack (1983). These methods calculate standardized variances in allele frequency change at polymorphic loci sampled at two or more different times. These variances provide an estimate of genetic drift which, in turn, is inversely related to N_e.

RESULTS

Allele Frequencies and Genetic Variability

Six of the 25 presumptive allozyme loci assayed were polymorphic in at least one of the populations sampled in 1991 (Table 2), and all populations conformed to Hardy-Weinberg expectations at these loci. The 10 sampled populations were fixed for the same alleles at all other loci analyzed. Mean observed heterozygosity estimates ranged from 0.014 in the Secret Pass population to 0.042 for the Nye Canyon population (Table 2).

Seven of the 25 presumptive allozyme loci assayed in the 1992 samples were polymorphic (Table 2), and all these samples conformed to Hardy-Weinberg expectations at all polymorphic loci. As in 1991, all populations were fixed for the same alleles at the monomorphic loci. Mean observed heterozygosity estimates ranged from 0.020 in the Nye Canyon population to 0.044 in the Sweetwater North population (Table 2).

Geographical Structure Among Colonies

Sample sizes for 1991 and 1992 collection efforts are given in Table 2. Five sites were repeat-sampled in 1992 (Sweetwater North and South, Nye Canyon, Reese River, and Kingston Canyon), and yearly allele frequencies for

TABLE 2. Sample sizes and allele frequencies at polymorphic loci assayed in *Speyeria nokomis apacheana* populations sampled in 1991 and 1992 with percent polymorphic loci (P) and direct count mean heterozygosity estimates (H).

		Western									Central		Eastern	
Sample site[a]		SWN	SWS	DG	NC	C108	ML	SC	RVC	LV	RR	KC	RV	SP
Sample size (1991)		21	42	18	20	10	20	0	0	0	58	34	17	14
Locus	Allele													
AAT-2	B	0.00	0.00	0.00	0.00	0.00	0.00	—	—	—	0.00	0.00	0.00	0.25
	C	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	1.00	1.00	1.00	0.75
GPI-1	C	1.00	1.00	0.94	1.00	1.00	1.00	—	—	—	1.00	1.00	1.00	1.00
	D	0.00	0.00	0.06	0.00	0.00	0.00	—	—	—	0.00	0.00	0.00	0.00
GPI-2	B	0.00	0.00	0.00	0.00	0.00	0.00	—	—	—	0.00	0.00	0.32	0.00
	C	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	1.00	1.00	0.68	1.00
MPI	C	0.62	0.88	0.94	0.62	1.00	0.97	—	—	—	1.00	1.00	1.00	1.00
	D	0.38	0.12	0.06	0.38	0.00	0.03	—	—	—	0.00	0.00	0.00	0.00
PGM	B	0.00	0.02	0.00	0.00	0.00	0.00	—	—	—	0.00	0.00	0.00	0.00
	C	0.74	0.33	0.47	0.60	0.45	0.32	—	—	—	0.81	0.26	0.32	1.00
	D	0.26	0.65	0.53	0.40	0.55	0.68	—	—	—	0.19	0.74	0.68	0.00
SOD	C	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	0.65	1.00	1.00	1.00
	D	0.00	0.00	0.00	0.00	0.00	0.00	—	—	—	0.35	0.00	0.00	0.00
P		8	8	12	8	4	8	—	—	—	8	4	8	4
H		0.036	0.024	0.027	0.042	0.020	0.016	—	—	—	0.032	0.016	0.028	0.014
Sample size (1992)		37	32	0	10	0	0	48	80	13	33	31	0	0
Locus	Allele													
GPI-1	C	1.00	1.00	—	1.00	—	—	1.00	1.00	1.00	0.98	1.00	—	—
	D	0.00	0.00	—	0.00	—	—	0.00	0.00	0.00	0.02	0.00	—	—
GPI-2	B	0.00	0.08	—	0.00	—	—	0.00	0.00	0.00	0.00	0.00	—	—
	C	1.00	0.92	—	1.00	—	—	1.00	1.00	1.00	1.00	1.00	—	—
MDH-1	B	0.00	0.00	—	0.00	—	—	0.00	0.00	0.00	0.02	0.00	—	—
	C	1.00	1.00	—	1.00	—	—	1.00	1.00	1.00	0.98	1.00	—	—
MPI	C	0.62	0.84	—	0.75	—	—	0.83	0.99	1.00	1.00	1.00	—	—
	D	0.27	0.04	—	0.05	—	—	0.17	0.01	0.00	0.00	0.00	—	—
	E	0.11	0.12	—	0.20	—	—	0.00	0.00	0.00	0.00	0.00	—	—
PGD	B	0.00	0.00	—	0.00	—	—	0.00	0.01	0.00	0.00	0.00	—	—
	C	1.00	1.00	—	1.00	—	—	1.00	0.99	1.00	0.97	0.95	—	—
	D	0.00	0.00	—	0.00	—	—	0.00	0.00	0.00	0.03	0.05	—	—
PGM	B	0.00	0.11	—	0.00	—	—	0.00	0.08	0.12	0.00	0.00	—	—
	C	0.69	0.33	—	0.90	—	—	0.56	0.28	0.58	0.98	0.35	—	—
	D	0.31	0.56	—	0.10	—	—	0.44	0.64	0.30	0.02	0.65	—	—
SOD	C	1.00	1.00	—	1.00	—	—	1.00	1.00	1.00	0.61	1.00	—	—
	D	0.00	0.00	—	0.00	—	—	0.00	0.00	0.00	0.39	0.00	—	—
P		8	8	—	8	—	—	8	12	4	20	8	—	—
H		0.044	0.032	—	0.020	—	—	0.034	0.023	0.022	0.021	0.022	—	—

[a]Sample sites: SWN = Sweetwater North, SWS = Sweetwater South, DG = Devil's Gate, NC = Nye Canyon, C108 = Cal Rt 108, ML = Mono Lake, SC = Scossa Ranch, RVC = Round Valley, CA, LV = Lee Vining, RR = Reese River, KC = Kingston Canyon, RV = Ruby Valley, SP = Secret Pass.

TABLE 3. Unbiased genetic distances (Nei 1978) above diagonal and unbiased genetic identities (Nei 1978) below diagonal for 13 Great Basin populations of *Speyeria nokomis apacheana* sampled in 1991 and 1992.

Population	SWS	SWN	DG	NC	C108	ML	SC	RVC	LV	RV	SP	RR	KC
Sweetwater South	*****	0.007	0.000	0.006	0.000	0.000	0.002	0.000	0.003	0.004	0.020	0.017	0.001
Sweetwater North	0.993	*****	0.005	0.000	0.007	0.010	0.002	0.011	0.005	0.015	0.011	0.012	0.011
Devil's Gate	1.000	0.995	*****	0.004	0.000	0.000	0.000	0.001	0.001	0.005	0.014	0.012	0.001
Nye Canyon	0.994	1.000	0.996	*****	0.006	0.008	0.001	0.009	0.004	0.013	0.009	0.010	0.010
CA Rt. 108	1.000	0.993	1.000	0.994	*****	0.000	0.001	0.000	0.001	0.004	0.014	0.012	0.000
Mono Lake	1.000	0.990	1.000	0.992	1.000	*****	0.003	0.000	0.004	0.004	0.021	0.018	0.000
Scossa Ranch	0.998	0.998	1.000	0.999	0.999	0.997	*****	0.003	0.001	0.007	0.011	0.011	0.004
Round Valley	1.000	0.989	0.999	0.991	1.000	1.000	0.997	*****	0.004	0.004	0.022	0.019	0.000
Lee Vining	0.997	0.995	0.999	0.996	0.999	0.996	0.999	0.996	*****	0.008	0.008	0.008	0.004
Ruby Valley	0.996	0.985	0.995	0.987	0.996	0.997	0.993	0.996	0.992	*****	0.025	0.022	0.004
Secret Pass	0.981	0.989	0.987	0.991	0.986	0.979	0.989	0.979	0.992	0.975	*****	0.008	0.022
Reese River	0.983	0.988	0.988	0.990	0.988	0.982	0.989	0.982	0.992	0.978	0.992	*****	0.019
Kingston Canyon	0.999	0.989	0.999	0.990	1.000	1.000	0.996	1.000	0.996	0.996	0.978	0.981	*****

these populations were pooled to represent an intergenerational mean that can be used to calculate genetic distances among the sampled populations. A UPGMA phenogram based on Nei's (1978) unbiased genetic distances (Table 3) did not represent the geographical relationships of the assayed populations particularly well (Fig. 2). For example, Secret Pass, an eastern population, clustered on the UPGMA phenogram most closely with Reese River, a central population. Similarly, Kingston Canyon, a central population, clustered among a group of western populations in the phenogram. Because of the nonconcordance of the phenogram in Figure 2 with the geographical dispersion of the populations (Fig. 1), we undertook a more detailed analysis of the genetic structure of the sampled populations.

Genetic Structure Among and Within Regions

Significant heterogeneity in allele frequencies (X^2 test, $p < .05$) at all polymorphic loci among all sampled populations in both years of sampling indicated substantial population structuring. When regions were considered independently, significant levels of heterogeneity in allele frequencies were observed among the populations within each region. Hierarchical F-statistics also pointed to fine-scale population structuring within regions for both years. For example, the 1991 within-region fixation index was 0.227. Using the relationship $F = 1/(1 + 4Nm)$ (Slatkin 1987), we arrive at a figure suggesting an average of only 0.851 individuals dispersed between colonies within each region in 1991.

The six 1991 western samples were subjected to a simultaneous test procedure (Sokal and Rohlf 1981) to obtain further insight into the geographic structures among them. All populations were heterogeneous except two groups. The first, consisting of California Route 108, Devil's Gate, Mono Lake, and Sweetwater South, was found to be homogeneous with respect to allele frequencies across two of the three (MPI and PGM) polymorphic loci in the samples. The greatest linear distance between any pair of these populations is approximately 46 km (Fig. 1). The mean F_{st} among the four populations was 0.022. The second homogeneous group consisted of Nye Canyon and Sweetwater North, two populations separated by 2 km of apparently suitable habitat (Fig. 1). The mean F_{st} estimate for these two populations was 0.010.

The simultaneous test procedure revealed no homogeneous groups among the 1992 western populations. Nye Canyon and Sweetwater

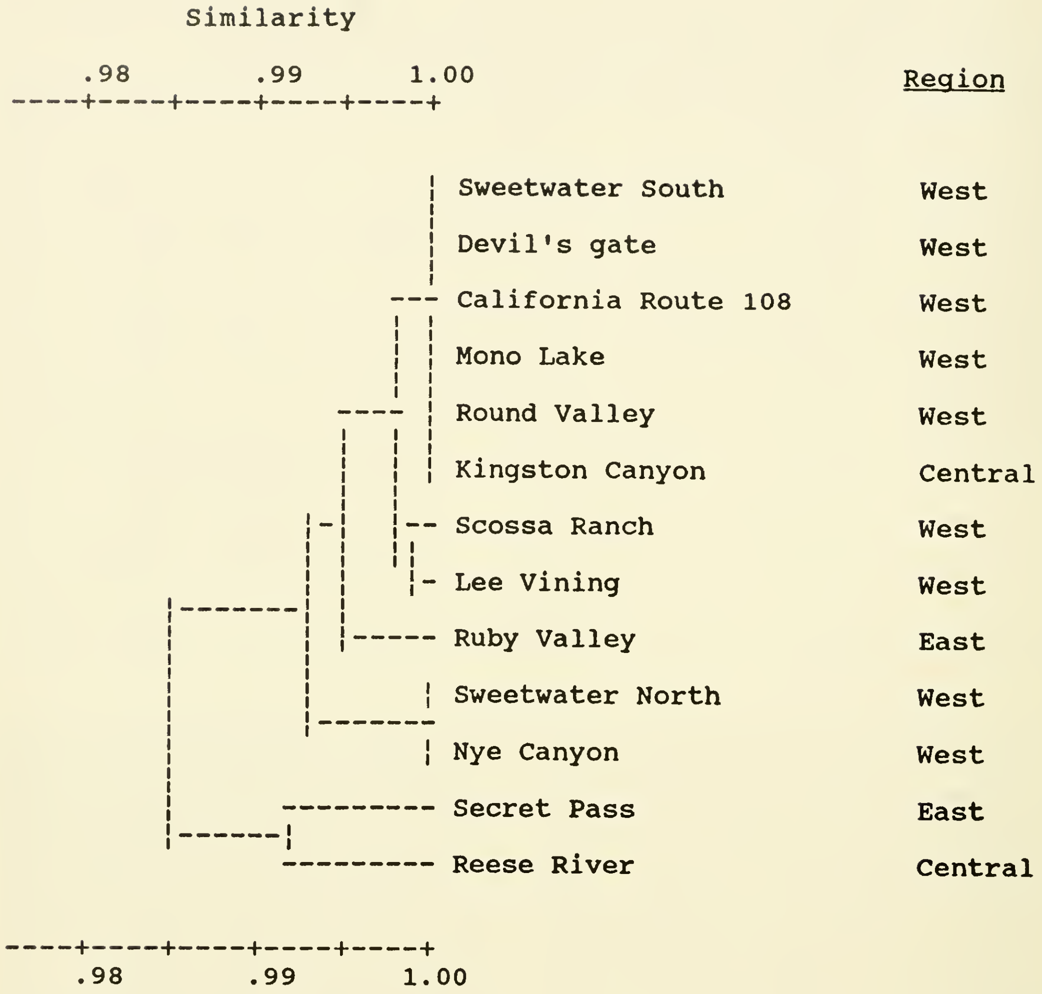
Similarity
.98
.99
1.00
Region
Sweetwater South
West
Devil's gate
West
California Route 108
West
Mono Lake
West
Round Valley
West
Kingston Canyon
Central
Scossa Ranch
West
Lee Vining
West
Ruby Valley
East
Sweetwater North
West
Nye Canyon
West
Secret Pass
East
Reese River
Central
.98
.99
1.00

Fig. 2. UPGMA phenogram based on Nei's (1978) unbiased genetic identities for 13 Great Basin populations of *Speyeria nokomis apacheana.* Regional designations indicate that topology of the phenogram does not correspond to the geographic arrangement of the populations. Cophenetic correlation coefficient is 0.873.

North formed a marginally heterogeneous group (total X^2 for two loci = 8.45, df = 3, p = .04) with a mean F_{st} estimate of 0.05 (*Nm* = 4.7; Slatkin 1987).

Estimates of Effective Population Size

Five *Speyeria nokomis apacheana* populations, Sweetwater North and South, Nye Canyon, Reese River, and Kingston Canyon, provided large enough samples in 1991 and 1992 (Table 2) to allow estimation of N_e's using the methods of Nei and Tajima (1981) and Pollack (1983). Estimates of N_e derived from both methods for replicated samples are given in Table 4. Estimates were smaller than the number of individuals sampled at each site. The large confidence intervals around these estimates (Table 4) result from the small number of alleles used in their estimation and the small number of generations (n = 1) over which the study was conducted (Nei and Tajima 1981, Pollack 1983, Waples 1989). Despite these limitations, the estimates are consistent with the high degree of structuring observed and indicate that the N_e's of *Speyeria nokomis* in the Great Basin are generally small.

DISCUSSION

Mean population heterozygosity estimates for *Speyeria nokomis apacheana* are consistently lower than heterozygosity in other

TABLE 4. Estimates of effective population sizes (N_e's) for five repeat-sampled *Speyeria nokomis apacheana* populations collected in 1991 and 1992. Confidence intervals are in parentheses.

Population	Estimates of N_e	
	Nei and Tajima (1981)	Pollack (1983)
Sweetwater North	36 (4–∞)	10 (0–37)
Sweetwater South	9 (2–∞)	6 (0–17)
Nye Canyon	2 (0–∞)	1 (0–4)
Reese River	4 (1–∞)	3 (0–11)
Kingston Canyon	73 (3–∞)	70 (0–1118)

nymphalid butterflies. For example, Brussard et al. (1989) estimated a range of mean heterozygosities of 0.17–0.26 among western North American populations in a complex of semispecies within the highly variable species *Euphydryas chalcedona*. Britten et al. (1993) estimated mean heterozygosities of 0.041-0.127 in Canadian *Boloria improba*, and 0.031 for the closely related, endangered, and narrowly endemic butterfly *Boloria acrocnema* (Britten et al. 1994); both values are near the high range of estimates for those of *Speyeria nokomis* in the Great Basin (Table 2). In addition, Brittnacher et al. (1978) estimated that mean heterozygosity in a number of California *Speyeria* species and subspecies ranged from 0.141 in *Speyeria coronis coronis* to 0.067 in *Speyeria atlantis*. Brittnacher et al. (1978) estimated a mean heterozygosity of 0.034 for *Speyeria nokomis apacheana* at Round Valley, a figure somewhat higher than our estimated heterozygosity for that population (0.023, Table 2), but within the range of estimates made herein for other *Speyeria nokomis apacheana* populations (Table 2).

A number of evolutionary forces could be responsible for the apparent lack of heterozygosity in the sampled *Speyeria nokomis apacheana* populations. Selection against heterozygous individuals is theoretically capable of reducing heterozygosity. There is, however, little indication that selection acts frequently on allozymes. Furthermore, selection is weak relative to genetic drift in small populations (Crow 1986, Hartl and Clark 1989).

Because genetic drift in small, isolated populations can erode heterozygosity over numbers of generations (Hartl and Clark 1989), it is the most plausible explanation for the observed low levels of isozyme variability in the *Speyeria nokomis* populations included in this study. Drift is most effective in eroding heterozygosity and causing loss of neutral alleles when populations are small and isolated. *Speyeria nokomis* populations in the Great Basin appear to meet both criteria. Although fairly large sample sizes were obtained at several sites, much smaller samples were taken at most sites with similar collecting efforts (Table 2). Sample size, therefore, is a rough indicator of relative population size, and most populations appeared to consist of far fewer than 100 individuals on the days they were sampled. Estimates of N_e (Table 4) corroborate the evidence for small effective population sizes in this taxon.

Several authors (e.g., Frankel and Soulé 1981, Allendorf 1986, Hedrick and Miller 1992) have stressed the importance of drift in the loss of selectively neutral alleles from populations subjected to bottlenecks. Populations with chronically small sizes may be considered analogous to populations that have suffered a series of bottlenecks. In that light, larger *Speyeria nokomis* populations would be expected to retain a larger complement of alleles over longer periods of time than would smaller ones.

Furthermore, allele frequencies are expected to fluctuate less between generations when N_e's are consistently large. This hypothesis is partially testable by comparing the results of our study with those of Brittnacher et al. (1978) for the Round Valley population. Brittnacher et al. (1978) collected 58 *Speyeria nokomis* from this colony in 1974 and 1975. A single locus (PGM) was polymorphic with the following allele frequencies: 0.69 for "PGM97," 0.23 for "PGM100," and 0.08 for "PGM103" (Brittnacher et al. 1978). Based on relative migration rates of alleles within each study, PGM97, PGM100, and PGM103 are assumed to be homologous with PGMD, PGMC, and PGMB, respectively, of the present study. As shown in Table 2, allele frequencies at the PGM locus have changed little in this large colony over the 18 years intervening between the two studies. In contrast, the Reese River sample, with an estimated N_e of 3–4 (Table 4), experienced some rather large changes in allele frequencies at several loci in the short interval between the 1991 and 1992 generations (Table 2).

Dispersal among butterfly colonies is expected to ameliorate the erosive effects of genetic drift in individual populations. Heterogeneity tests and F-statistics, however, suggest that *Speyeria nokomis* colonies are generally isolated from each other and that even geographically proximate populations are likely to be drifting independently. Even though the 1991 data suggest that two sets of populations were homogeneous and that there was substantial gene flow among them (Slatkin 1987), sample sizes from these populations were necessarily small and the resultant power of the G-test (Sokal and Rohlf 1981) to detect heterogeneity among allele frequencies was low (mean power for pairwise G-tests = 0.046). Thus, the apparent homogeneity and implied high rate of gene flow among these populations may not be real. Alternatively, dispersal rates among colonies may change between years depending on weather or other environmental conditions. In any case, colonies are not static; the number of individuals dispersing among colonies apparently changes from generation to generation. This situation probably reflects environmentally mediated fluctuations in population sizes and resource availability.

The results of this study further confirm that *Speyeria nokomis* populations are confined to mesic seep, spring, and riparian areas in the Great Basin. Such habitats are often separated by tens of kilometers of unsuitable habitat in which individual butterflies have never been observed. The isozyme data presented here indicate very low levels of gene flow among the sampled populations and suggest that these populations may have lost genetic variability as a result of small effective sizes and genetic drift. Because a number of unique alleles were detected in several populations (Table 2), conservation of individual colonies may be important to the evolutionary potential of this subspecies (Frankel and Soulé 1981, Allendorf 1986). The apparent philopatric nature of this butterfly results in genetically unique colonies whose habitat should be preserved in order to achieve this goal.

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INFLUENCE OF FINE SEDIMENT ON MACROINVERTEBRATE COLONIZATION OF SURFACE AND HYPORHEIC STREAM SUBSTRATES

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ABSTRACT.—Colonization of macroinvertebrates was assessed in a stream impacted by inputs of fine sediments. Colonization was examined at the stream surface and within the hyporheos with Whitlock-Vibert (W-V) boxes. Hyporheic areas accumulated much greater amounts of all size categories of sediment. No significant difference was observed in the amounts of organic matter accumulated at either depth. Only 150-μm sediment had significant effects on macroinvertebrate total numbers and number of taxa. Total numbers of invertebrates at 30 cm were only 20% of those at the surface. Canonical Correspondence Analysis indicated that the strongest influence on macroinvertebrates colonizing W-V boxes at the surface was stream size and secondarily fine sediments. Within the hyporheos, abundance of fine sediment was the dominant influence on macroinvertebrate assemblages. Impacts of sedimentation on hyporheic environments can have significant and persistent impacts on streams.

Key words: stream ecology, hyporheos, sediment, organic matter, macroinvertebrate.

The addition of fine substrates to streams can result in significant changes to stream macroinvertebrate assemblages. Substrate plays an important role in structuring stream macroinvertebrate assemblages. Numerous studies (see Minshall 1984) have demonstrated the importance of both substrate type and size in determining distributions of specific taxa. In general, the number of taxa and productivity of substrates composed of small particle sizes are less than those of larger, more heterogeneous substrates (Pennak and Van Gerpen 1947, Allan 1975, Ward 1975). Reduced invertebrate utilization and production from small substrates may be attributed to a variety of reasons, ranging from the need of some insects for large particles for attachment, to the need for interstitial pore space for movement among substrate particles. Macroinvertebrate responses to variation in substrate size and composition can result in distribution patterns that are observed within streams longitudinally (Allan 1975) and among several streams within a region (Richards et al. 1993).

The addition of fine substrates to streams may also affect macroinvertebrate abundance and distribution in the hyporheos. Taxa within the hyporheic region of streams can be found as deep as 70 cm below the stream bottom (Williams and Hynes 1974). The benthic assemblage within the hyporheic region is associated with overall stream productivity and surface assemblage structure (Strommer and Smock 1989, Ward 1989). Because macroinvertebrates utilize the hyporheos during all seasons, this area can provide a refuge for new colonists following high flows or other disturbance events (Williams 1984, Palmer et al. 1992). Alterations to physical characteristics of the hyporheos could cause significant changes in the dynamics of macroinvertebrate populations that utilize these areas.

This study was undertaken to determine whether fine sediment inputs from both point and nonpoint sources influenced macroinvertebrate assemblages along the length of a stream in central Idaho. We hypothesized that assemblage structure could be related to the proportion of fines in surface and hyporheic substrates.

METHODS

Study Area

The study was conducted in Bear Valley Creek, a headwater tributary to the Middle Fork of the Salmon River watershed in central Idaho. The stream flows through subalpine meadows and lodgepole pine (*Pinus contorta*) forests on a granitic batholith. Alluvial deposits of erosive sandy soils typify the region. Historically, the stream had high secondary productivity and supported large populations of anadromous salmonids. Since the 1950s, however, large volumes of fine, inorganic sediments have entered the stream through both point and nonpoint sources along the length of the stream (Konopacky et al. 1986). Consequently, stream substrates have high proportions of fine sediments in many areas, and fish production has declined partly as a result of sediment introduction.

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Experimental Method

To examine whether sediment influences macroinvertebrates assemblages, we conducted colonization studies at 19 sites along a 50-km section of Bear Valley Creek. Colonization studies are effective means of examining the dynamics of stream macroinvertebrate assemblages and have been used extensively in many streams and geographic areas (Robinson et al. 1990, Mackay 1992). Study sites were located in riffle habitats at approximately even intervals along the length of the stream. Sites reflected the full range of substrate characteristics found in the stream, including low proportions of fine sediments and high proportions of sediments.

At each site, stream width, gradient, and substrate composition were assessed. Substrate was assessed by determining the proportion of surface particles <4 mm in diameter. One hundred points were randomly selected along a transect that bisected the study riffles, and the closest substrate particle to each point was measured. This size class corresponds well to proportions of smaller-sized surface substrate particles in Bear Valley Creek (Konopacky et al. 1986).

We used small basket samplers (Whitlock-Vibert [W-V] boxes; Wesche et al. 1989) for macroinvertebrate colonization. The polypropylene (14 × 6.4 × 8.9-cm-deep) boxes enclosed a known volume of standardized substrate that allowed comparisons among sites. These boxes are typically used to incubate fish eggs in stream gravels (Federation of Fly Fishermen personal communication). The sides, top, and bottom of the boxes are perforated with rectangular slots (3.5 × 13 mm) to allow water circulation. The bottom of each box was covered with duct tape to reduce sediment loss. Boxes were filled with 3/4-inch-grade clean gravel. This readily available substrate approximates the size of clean gravels in Bear Valley Creek. Two boxes were placed at each site: one approximately 30 cm below the surface of the substrate (using a small shovel) and the other flush with the surface directly above the below-surface box. Both boxes were located in the center of the stream channel. Boxes were placed in the substrate the last week of July 1988 and retrieved 10 weeks later. During this period little or no rainfall was received in the area, and the stream was in a baseflow condition.

Colonization was examined in relation to variation in fine sediments that accumulated in the boxes. Fine sediment accumulation in W-V boxes has been shown to be correlated with the amount of fines in surrounding substrates in streams and laboratory channels (Wesche et al. 1989). W-V boxes were removed from the stream as carefully as possible so as to retain any fine substrate materials and macroinvertebrates in the boxes. While still under water, the W-V box was slipped into a plastic bag with minimal disturbance. The lower box was removed in the same way after excavating the substrate material between the upper and lower boxes. Material from the boxes was preserved in 10% formalin. In the lab the 3/4-inch-grade gravel was removed from the samples with a large sieve. Macroinvertebrates were removed from these samples under a dissection microscope, identified to family, and enumerated. The remaining material was divided into portions that collected on 150-μm and 850-μm sieves. These portions were dried at 60°C and then ashed in a muffle furnace to obtain a weight for organic and inorganic (fine sediment) fractions. The 850-μm sieve collected material ≤ 3.5 mm in diameter. Sediment particle sizes <4 mm are frequently implicated in negative impacts on the abundance of stream invertebrates and productivity (Nuttall 1972, Alexander and Hansen 1986). Smaller particle sizes (<850 μm) include clay-sized particles that also decrease invertebrate abundance (Cederholm and Lestelle 1974) and clog interstitial spaces.

Differences in sediment and organic accumulation between surface and below-surface boxes were examined by group comparisons, as were macroinvertebrate assemblage comparisons (species richness, total numbers).

Macroinvertebrate assemblage composition among the sites was examined with multivariate direct gradient analysis (Canonical Correspondence Analysis; ter Braak 1986, 1987). Macroinvertebrate data were log transformed prior to analysis. In CCA, axes are selected to be linear combinations of environmental variables so that taxa are related directly to a set of these variables. This technique is particularly useful for examining the relative strength of various environmental variables on influencing assemblage composition (ter Braak and Prentice 1988, Richards et al. 1993). Environmental variables used in the analysis were sediment and organic accumulations in the boxes, proportion of 4-mm surface sediments in riffles, gradient, and stream width. The latter two variables were included to account for some differences in stream size and channel morphology among the sites.

RESULTS

The width of the study sites ranged from 2.9 to 24 m (mean = 8.57). The proportion of sediments <4 mm in diameter in riffles varied from 0 to 56% (mean = 8.6); all sites had gradients <2% (mean = 0.47).

A much larger amount of fine sediment accumulated in the below-surface boxes than in the surface boxes (*t* test, $p < .05$; Table 1). This was true for both the 850-μm and 150-μm size classes. There was no significant difference in the amounts of organic material that accumulated between treatments for either size class.

Twenty-two macroinvertebrate families were identified from the W-V samplers (Table 2). With the exception of Perlidae, Ceratopogonidae, and Tabanidae, all taxa were found in both surface and below-surface locations. Significantly ($p < .05$) greater numbers of taxa and total numbers of individuals per box were found in the surface samples (Table 2). The most abundant taxa in below-surface samples were Heptageniidae, Leptophlebiidae, Chloroperlidae, and Chironomidae. These taxa also had relatively high abundance in surface samples. Baetidae and Ephemerillidae had relatively high abundance in the surface samples but were not well represented in below-surface samples. No taxa were more abundant in below-surface samples than in surface samples.

Pearson correlation coefficients were calculated between each size class of sediment and taxa richness and total number of individuals to determine whether fine-sediment variables had relationships to macroinvertebrate assemblage characteristics. Separate calculations were made for surface and below-surface samples. No significant correlations ($p < .05$) were found with surface samples. In below-surface samples a significant correlation ($p < .05$) was observed between the 0.15-mm sediment size class and both number of taxa and total numbers of individuals (Fig. 1), but no significant correlations were found with the 0.85-mm size class.

Results of the CCA analysis for surface samples indicated that sediment accounted for a relatively small proportion of the variance in assemblage composition among sites. The first axis, which described the greatest amount of variation in the ordination, was most strongly influenced by gradient and width (Table 3). This axis differentiated the taxa most abundant at sites with high stream gradient and narrow widths from those taxa most abundant at sites with low gradient and wide widths. These data suggest that longitudinal position of the station along the stream course played the greatest role in determining assemblage composition. Nematodes, Ceratopogonidae, Hydropsychidae, and Pteronarcyidae were found in narrow, high-gradient sites, and Rhyacophilidae and Hydracarina were found at

TABLE 1. Macroinvertebrate numbers and sediment and organic material accumulations in experimental colonization boxes. * denotes a significant difference ($p < .05$, *t* test) between surface and below-surface boxes.

	Surface		Below-surface	
Variable	Mean	Std. dev.	Mean	Std. dev.
850-μm sediment* (gr/box)	11.01	11.22	101.01	51.04
150-μm sediment* (gr/box)	11.44	17.98	79.76	50.74
850-μm organic (gr/box)	0.435	0.460	0.572	0.359
150-μm organic (gr/box)	0.643	0.679	0.706	0.438

Table 2. Macroinvertebrate taxa that colonized surface and below-surface W-V boxes.

	Surface		Below-surface	
Taxa	Mean	Std. dev.	Mean	Std. dev.
Baetidae (BAE)	38.02	50.13	3.84	8.51
Ephemeriliidae (EPH)	35.49	45.53	3.50	5.05
Heptageniidae (HEP)	54.81	60.59	10.96	27.68
Leptophlebiidae (LET)	36.05	37.96	23.80	25.70
Siphlonuridae (SIP)	7.89	20.03	2.96	6.78
Brachycentridae (BRA)	5.81	15.96	0.11	0.48
Hydropsychidae (HYD)	1.75	6.66	0.22	0.66
Hydroptilidae (HYP)	10.03	20.78	0.22	0.66
Lepidostomidae (LEP)	58.28	106.43	2.19	4.52
Limniphilidae (LIM)	12.58	18.95	1.53	3.00
Rhyacophilidae (RHY)	0.66	1.96	0.11	0.48
Chloroperlidae (CHL)	27.35	28.25	12.01	11.75
Perlidae (PED)	0.77	1.88	0.00	0.00
Perlodidae (PER)	5.47	8.27	0.77	1.98
Pteronarcyidae (PTE)	0.77	1.73	0.11	0.48
Ceratopogonidae (CER)	0.55	1.94	0.00	0.00
Chironomidae (CHI)	718.15	868.08	414.84	618.80
Tabanidae (TAB)	3.40	13.82	0.00	0.00
Tipulidae (TIP)	9.65	16.35	5.38	10.08
Elmidae (ELM)	9.75	23.07	2.74	5.24
Annelid (ANN)	10.44	28.29	1.33	2.54
Mollusca (MOL)	11.07	34.45	3.40	7.64
NUMBER TAXA/BOX	11.3	3.24	7.0	2.62
TOTAL NUMBER/BOX	1120.3	1087.5	492.8	641.33

low-gradient, wide sites (Fig. 2). The second axis was most strongly influenced by total organic weight and width. No environmental variables had strong ($r < .35$) correlations with the third axis.

Sediment was more important in defining differences in assemblage composition among below-surface samples. The 0.85-mm and 0.15-mm sediment volumes had highest correlations with the first CCA axis (Table 3). These variables acted in an opposite manner. The majority of taxa were associated with decreasing amounts of 0.15-mm sediment; however, Brachycentridae and Hydroptilidae were most abundant at sites with relatively high amounts of 0.15-mm sediment (Fig. 2). Gradient and width had the highest correlations with the second axis. There appeared to be little correspondence between taxa preferring high-gradient, narrow sites or low-gradient, wide sites in below-surface samples and above-surface samples (Fig. 2). Taxa preferring high-gradient sites were Mollusca, Perlodidae, and Tipulidae. Hydracarina, Elmidae, and Siphlonuridae preferred wide, low-gradient sites. As with surface samples, the third axis was difficult to interpret.

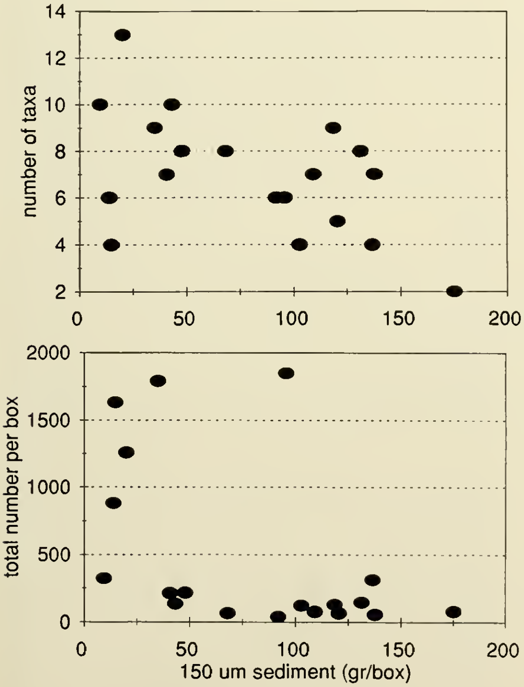

Fig. 1. Correlations between number of taxa ($r = -.52$, $p < .05$) and total numbers of individuals ($r = -.48$, $p < .05$) and the amount of fine sediment that accumulated in W-V boxes within the hyporheos.

TABLE 3. Correlations between environmental variables and CCA axes. Percentages refer to the proportion of variance in species data explained.

Above surface	Axis 1 (17.3%)	Axis 2 (9.6%)	Axis 3 (8.0%)
Surface sediment (<4 mm)	0.01	0.32	0.17
Box sediment (850 μm)	0.14	0.29	−0.13
Box sediment (150 μm)	−0.28	0.19	0.06
Total organic weight	0.03	0.64	0.13
Gradient	0.51	−0.47	−0.28
Width	−0.53	0.53	−0.32
Below surface	**Axis 1 (9.3%)**	**Axis 2 (7.5%)**	**Axis 3 (6.0%)**
Surface sediment (<4 mm)	−0.10	0.17	0.30
Box sediment (850 μm)	0.40	0.34	−0.03
Box sediment (150 μm)	−0.60	−0.01	0.17
Total organic weight	0.28	0.38	0.38
Gradient	0.02	0.60	−0.18
Width	−0.10	−0.61	0.42

DISCUSSION

Colonization patterns on the stream surface were most strongly influenced by variation among sites with respect to stream size and gradient and not fine-sediment abundance. Several other studies within the Middle Fork of the Salmon River basin also found that macroinvertebrate assemblages exhibit predictable changes with increasing stream size (Bruns et al. 1982, 1987, Bruns and Minshall 1985). In our study the available pool of colonists probably shifted within the study area and masked our ability to examine fine-sediment impacts. Within the 60-km study region on Bear Valley, the stream increases from a first- to a fourth-order stream and exhibits longitudinal changes in channel morphology and riparian characteristics along this gradient that influence macroinvertebrate assemblage composition (Bruns et al. 1982, 1987). Surface substrate characteristics played a secondary role to other stream features in influencing macroinvertebrate abundance. However, this does not mean that substrates do not influence macroinvertebrate distributions on surface substrates. Other studies of sediment effects in the Bear Valley watershed found that biomass of macroinvertebrate drift from sand substrates was less than that from larger substrates (Konopacky 1984) and that macroinvertebrate densities were greater in riffles with low amounts of fines than riffles with higher proportions (Bjornn et al. 1977). Both studies were conducted within relatively small areas that did not encompass longitudinal variation in stream characteristics.

Fine-sediment abundance did have distinct effects on macroinvertebrate colonization within the hyporheos. The greatest effect was with the smallest sediment size class (<1.50 mm). Sediment particles in this size range may have the most potential for clogging interstitial spaces within gravel. Although most sediment studies have not explicitly assessed impacts of sediments in this size range on macroinvertebrates, at least one study (Cederholm and Lestelle 1974) noted that particles <0.84 mm in diameter had strong negative correlations with total number of stream invertebrates. In addition, particles <1 mm in diameter are known to reduce availability of dissolved oxygen in stream gravels (Tagart 1984), and clay-sized silt impairs periphyton production in riffles (Graham 1990).

Our results suggest that macroinvertebrate habitat in Bear Valley Creek is impaired because of fine-sediment abundance in the hyporheos. Cobble and gravel bed streams without high proportions of sediment in the hyporheos typically exhibit much less difference in macroinvertebrate composition and abundance between surface and hyporheic zones than we observed in this study. For example, Coleman and Hynes (1970) found little differentiation in macroinvertebrate numbers in the upper 30 cm of substrate. Williams and Hynes (1974) reported differences among near-surface and below-surface macroinvertebrate assemblages; however, they found total numbers at 30-cm depth were typically at least 50% of those near the surface. In Bear Valley, total numbers at 30 cm were only 22% of those near the surface. Bear Valley

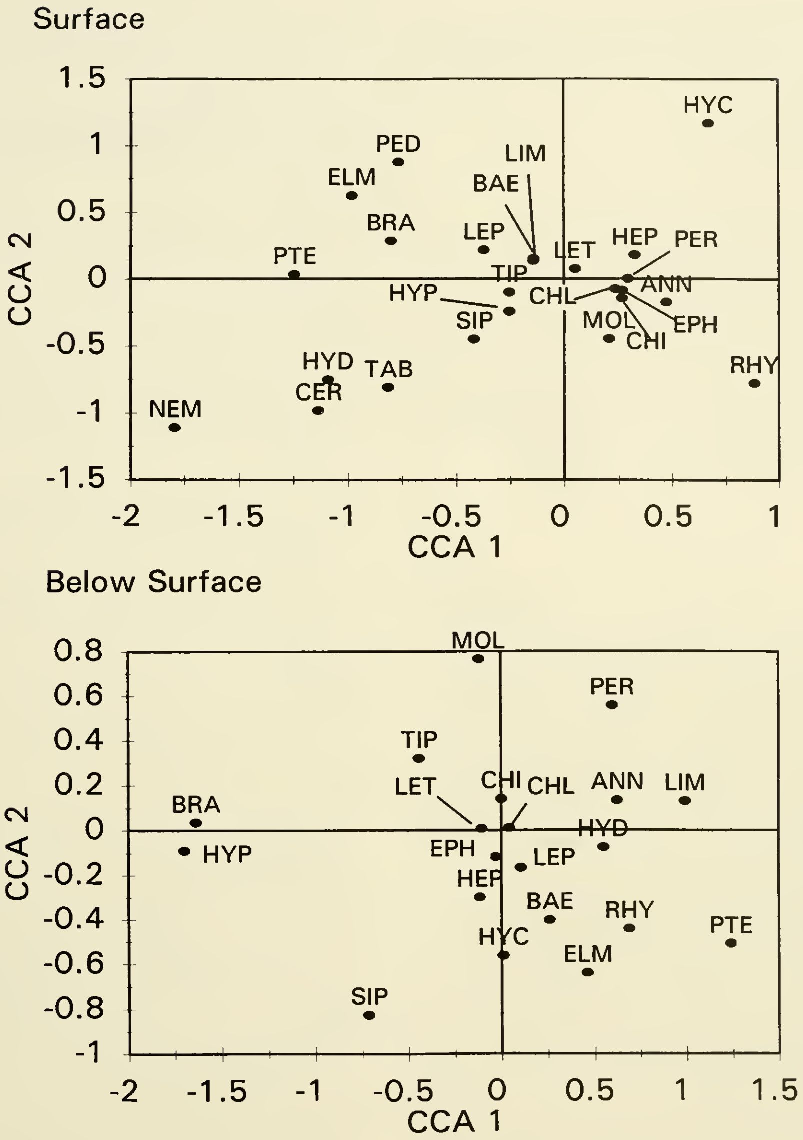

Fig. 2. Ordination of macroinvertebrate taxa with respect to environmental variables in surface and hyporheic areas.

results are more similar to those reported from streams with high proportions of fine sediment in the hyporheos, such as those examined by Poole and Stewart (1976) and Strommer and Smock (1989), who found that total numbers at approximately 30-cm depth were at least 80% less than those near the surface. Both studies attributed these differences to high proportions of fines in the hyporheos that altered physical habitat and subsurface water flow.

High proportions of fine sediment within the hyporheos of Bear Valley Creek may significantly decrease available habitat for macroinvertebrates and therefore limit potential secondary production in the stream. Our study suggests that the hyporheos should be included when assessing impacts of sediment additions to stream ecosystems. Since macroinvertebrate assemblages exhibit consistent long-term changes to watershed activities that influence substrate characteristics

(Richards and Minshall 1992), dramatic and potentially persistent effects can be initiated through the introduction of fine sediments into the hyporheos.

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RESOURCE OVERLAP BETWEEN MOUNTAIN GOATS AND BIGHORN SHEEP

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ABSTRACT.—Mountain goat (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*) ranges overlap substantially in northwestern United States and southwestern Canada. Resource overlap in food and habitat parameters is assumed, but the degree of overlap has not been estimated. Data from published separate and comparative studies on food and habitat use were used to calculate indices of resource overlap for goats and sheep. Indices of overlap for general forage classes (grasses, forbs, browse) were >0.90 in summer and winter for data based on pooled data from separate studies and in summer for data from comparative studies. In winter for comparative studies this overlap was 0.64. For studies where forage species were identified, estimates of resource overlap from separate studies were ~0.8 but were <0.5 for comparative studies. Indices of overlap for habitat variables were also low (<0.7) for comparative studies. It was concluded that possible overlap in food and habitat use by goats and sheep could be extensive; but in sympatric populations, resource overlap may be reduced substantially.

Key words: bighorn sheep, mountain goats, Oreamnos americanus, Ovis canadensis, *resource overlap, resource partitioning.*

In the northwestern United States, Rocky Mountain goats (*Oreamnos americanus*) historically ranged south along the Bitterroot Divide to near the Continental Divide between Idaho and Montana and in the Cascade Mountains south to central Washington (Hall 1981). With the gradual extension of European settlement, goats were extirpated from numerous areas. Beginning in the early 1900s, goats were transplanted into their historic range as well as other suitable habitats, e.g., Colorado, northwest Washington. Many of these areas where goats were not recently found were historic ranges of bighorn sheep (*Ovis canadensis*). The introduction of mountain goats into the range of bighorn sheep raised concerns regarding potential impacts of goats on bighorns. Because goats and sheep are generalist herbivores that use subalpine to alpine environments, it is commonly assumed their food and habitat requirements overlap extensively in these areas. Based on this assumption, some researchers have expressed concern that goats might compete with sheep when introduced into existing sheep range. Although the outcome of this competition is uncertain, goats are thought to be the superior competitors (Whitfield 1983). Concern about potential competition has caused a reevaluation of introducing goats into areas beyond their historic range, especially in areas containing bighorn sheep. However, resource overlap, which must not be confused with competition, does not justify sweeping generalizations about competitive interactions. Additionally, the assumption of extensive resource overlap is based primarily on food and habitat use by goats and sheep from studies separated by space and time. It is unclear whether data from such diverse studies can be used to infer resource overlap of these two species in sympatry. Consequently, the implication of competition between goats and sheep is tenuous and should not be used to influence reintroduction decisions without a review and reassessment of resource overlap between these two species.

There are many studies on food habits and habitat use of goats and sheep. However, most are unpublished theses. There has yet to be a comprehensive review of existing literature, nor have any estimates of resource overlap been reported. My objectives were to (1) review and summarize available literature on food and habitat utilization of Rocky Mountain goats and bighorn sheep and (2) reevaluate and quantify, if possible, the amount of resource overlap that exists between these two species. Only with such a review and reevaluation can we proceed to set up rigid experimental designs to address questions concerning potential competition between goats and sheep.

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METHODS

I compiled data from 34 separate studies on food habits and habitat use of sheep and goats and from 3 comparative studies of sympatric populations. Some separate studies were of known allopatric populations because the study areas were outside the range of the corresponding sheep or goat species. Most studies were in areas where both species occurred, but the reports did not indicate whether the corresponding species was in the study area. Because I could not assume allopatry in all studies, this term is not used in reference to these separate studies.

Methods of data collection varied among studies. Most authors expressed food habits as percentage of observed use or occurrence in stomach or feces but did not adjust their estimates for forage availability (Rominger and Bailey 1982). Some researchers classified forage only by classes (grass, forbs, or shrubs); others presented lists of forage species. Most researchers quantified diets separately for either summer or winter or both. A few researchers presented diets for spring and fall, but there were insufficient data to include these seasons in this analysis.

I expressed food habits data as percentage of use by category. I used these data to calculate resource overlap indices (O) based on equation 1 (Lawlor 1980):

$$o_{jk} = \Sigma\, p_{ij}\, p_{kj}\, [\Sigma(p_{ij})^2 * \Sigma(p_{kj})^2]^{1/2} \qquad [1]$$

Where: p_{ij} and p_{kj} are the proportions of resource type j used by species i and k.

The index O ranges from 0 (no overlap) to 1.0 (total overlap). Indices of overlap were calculated for all combinations of food categories (forage classes, species), season (winter, summer), and study status (separate, comparative) except specific winter diets from comparative studies for which no data were available. Pooled data from separate studies were used to calculate one set of resource overlap indices; data from comparative studies were used to determine additional indices for each study. Calculations of resource overlap for forage species from separate studies were limited to studies from subalpine and alpine areas in the northwestern U.S. where sheep and goats co-occur. Food habits reflect availability of food species (Rominger and Bailey 1982), which in more northern areas for goats and more southern areas or lower elevations for sheep can differ greatly, biasing any comparisons that might be made. Restricting this review to data from subalpine and alpine areas in the northwest region should limit differences in resource availability to an acceptable level.

Several investigators reported percentage of habitat utilized by goats and sheep. Comparing data from these studies was difficult because habitat classifications were not standardized. In these studies general patterns of habitat use were summarized. For the few comparative studies of sympatric populations, habitat overlap indices were calculated with equation 1. In separate studies some authors measured physical characteristics of the environment selected by animals, specifically, distance to escape cover, elevation, and slope. Data were not expressed in percent use of different categories but were means of observations. These data were compared with t test or analysis of variance designs as appropriate. The null hypothesis was no difference in means for goats and sheep for the tested characteristic. Acceptance of the null hypothesis would indicate total resource overlap. Rejection ($P < .05$) of the null indicates significant statistical separation along the tested resource axis.

RESULTS

Food Habits

Several investigators presented only qualitative assessments of goat and sheep diets (Davis 1938, Honess and Frost 1942, Spencer 1943, Casebeer 1948, Couey 1950, Smith 1954, McCann 1956, Berwick 1968, Cooperrider 1969). Diets were similar in summer and winter, with both species relying on grasses and forbs. Where authors estimated diet compositions, data indicated that goats relied on grasses (52%) and forbs (30%) in summer but shifted to grasses (60%) and shrubs (32%) in winter (Table 1). Sheep (Table 1) used mainly

TABLE 1. Summary of general forage classes used by goats and sheep from various studies in alpine and subalpine habitats. Estimates are expressed as percent of total use and are based on either fecal or rumen analyses. Locations of studies are indicated by standard U.S. Postal Service codes.

	Summer			Winter		
Species Reference	Grass	Forb	Browse	Grass	Forb	Browse
MOUNTAIN GOATS						
Saunders 1955 MT	76	14	2	59	10	30
Hibbs 1967 CO	97	3	0	88	0	12
Peck 1972 MT	22	78	0	90	6	1
Pallister 1974 MT	40	60	0			
Johnson et al. 1978 CO	60	29	7			
Thompson 1981 CO	84	15	1			
Thompson 1981 MT	11	9	79	47	2	51
Stewart 1975 MT	47	53	0			
Johnson 1983 WA	44	20	35	31	3	65
Campbell & Johnson 1983 WA	43	20	36			
Adams & Bailey 1983 CO				45	24	30
$\bar{x}$	52	30	16	60	8	32
BIGHORN SHEEP						
Mills 1937 WY	60	35	5	98	0	0
Moser 1962 CO	75	6	19			
Pallister 1974 MT	12	55	32	98	2	0
Frisina 1974 MT	95	4	1	92	6	1
Stewart 1975 MT	44	47	8	40	40	20
Todd 1975 CO	65	6	29	23	11	67
Johnson & Smith 1980 NM	46	50	4	83	10	7
Whitfield 1983 WY	25	12	63	30	32	39
Martin 1985 MT	74	16	10	39	50	10
Estes 1979 WA	30	8	62	62	3	35
Honess & Frost 1942 WY	51	30	19			
Harrington 1978 CO	88	12	0			
Kasworm et al. 1984 MT				65	12	23
Blood 1967 BC				54	5	40
Constan 1972 MT				72	17	8
Keating et al. 1985 WY				56	7	38
Schallenberger 1966 MT				87	9	2
Oldemeyer et al. 1971 WY				61	17	22
$\bar{x}$	56	23	21	64	15	21

grasses (56%) in summer but used forbs (23%) and shrubs (21%) more equally. Sheep also exhibited a seasonal change to grasses (65%) in winter.

Nine studies of goats and 11 studies of sheep contained analyses of forage species used. Although many plant species were used, most were consumed at very low levels (<1% of diet; Laundré 1990). Data were summarized for only those 12 genera that occurred ≥ 1% within the diet of at least sheep or goats (Table 2). The main genera used by goats and sheep in the summer were sedges (*Carex* sp.), wheatgrass (*Agropyron* sp.), bluegrass (*Poa* sp.), fescue (*Festuca* sp.), and bluebells (*Mertensia* sp.). Winter diets consisted mainly of sedges, wheatgrass, sagebrush (*Artemisia* sp.), and fescue.

Three studies (Pallister 1974, Stewart 1975, Dailey et al. 1984) presented data of food habits from sympatric populations of nonnative goats and native sheep. Pallister (1974) and Stewart (1975) primarily studied sheep but also recorded food habits of naturalized mountain goats in their study areas. The goats were descendants of releases made in the 1940s. Pallister (1974) found that summer diets of mountain goats consisted of 40% grasses and 60% forbs. During the same time sheep consumed 12% grasses, 55% forbs, and 32% shrubs. Although both species relied on forbs to a similar level, comparisons of forb species eaten indicated little overlap except clover (*Trifolium parryi*) (Pallister 1974: 48). Stewart (1975) found a similar reliance on grasses by sheep (44%) and goats (47%), but

TABLE 2. Comparison of percent use of preferred plant genera for goats and sheep. The percents are averages of the values reported in the literature.[a] Sample size (n) is the number of reported values used to calculate the means.

	Summer		Winter	
Species	Sheep ($n = 7$)	Goats ($n = 7$)	Sheep ($n = 10$)	Goats ($n = 5$)
Agropyron sp.	6	9	15	4
Carex sp.	15	10	15	8
Deschampsia sp.	2	<1	<1	<1
Festuca sp.	8	5	12	18
Poa sp.	15	14	1	4
Koeleria sp.	<1	5	3	1
Stipa sp.	<1	<1	2	<1
Artemisia sp.	<1	<1	10	3
Mertensia sp.	2	6	0	<1
Potentilla sp.	4	1	<1	<1
Salix sp.	5	4	1	1
Trifolium sp.	5	2	0	<1

[a] Mills 1937, Hibbs 1967, Oldemeyer et al. 1971, Constan 1972, Peck 1972, Pallister 1974, Frisina 1974, Stewart 1975, Johnson et al. 1978, Johnson 1983, Johnson and Smith 1980, M. J. Thompson 1981, Adams and Bailey 1983, Campbell and Johnson 1983, Whitfield 1983, Kasworm et al. 1984, Keating et al. 1985, Martin 1985

goats relied most on *Poa* sp. while sheep were more evenly divided among three species: *Agropyron*, *Carex*, and *Poa* (Stewart 1975: 68, 98). Overall forb use by sheep and goats was also similar, 47% for sheep, 53% for goats, but specific use of forbs differed. Sheep relied on a variety of forb species while goat diets consisted mostly of *Arnica latifolia* and *Erigeron* sp. Dailey et al. (1984) conducted parallel feeding trials with captive goats and sheep on unoccupied range in Colorado. Their work indicated goats ate more forbs in summer (goats 88%, sheep 70%) and winter (goats 59%, sheep 22%), while sheep consumed more grasses (summer, 30% vs. 11%; winter, 75% vs. 27%).

For summer diets expressed in forage classes, overlap indices were high for separate (0.98) and comparative studies (0.93) (Fig. 1a). Resource overlap in winter, based on data from separate studies, was also high (0.99). For the comparative study from Colorado (Dailey et al. 1984), the winter overlap index was 0.64 (Fig 1a). For the pooled separate studies where forage species were identified, summer (0.86) and winter (0.80) indices were slightly lower than those for general forage classes (Fig. 1a). Summer overlap indices (Fig. 1a) for the two comparative studies in Montana (Pallister 1974, Stewart 1975), however, were substantially lower (0.32 and 0.55) than those for general forage classes (Fig. 1a). There were insufficient data to determine whether indices from the comparative studies differed statistically from the general diet index.

General Habitat Use

Oldemeyer et al. (1971) divided habitat used by sheep in Yellowstone National Park into three general types: forest, grass, and shrub. In winter they found that sheep used forest 13%, grass 78%, and shrub 9% of the time. When they divided the area based on terrain, they found sheep used "steep" areas 39%, rocky outcrops 14%, ridgetops 36%, hilly areas 8%, and level areas 4% of the time. Of the numerous structural/vegetational formations defined by Martin (1985) in Montana, sheep spent most of their summertime in the "alpine turf" formation (approximately 50%) and the "sparsely vegetated dirt scree" formation (approximately 28%). In spring, Frisina (1974) found sheep 36% of the time in "rocky reef" and 59% in "bunchgrass" types. Sheep use of the rocky reef type in fall increased to 64% and decreased to 34% in the bunchgrass type. Tilton and Willard (1982) divided their Montana study area into rockland, shrub/grass, open forest, and closed forest habitat types. They found sheep spending 14% of their time in the rockland type, 46% in the shrub/grass, 40% in the open forest, and 1% in the closed forest types.

Peck (1972) divided goat habitat in Montana into four types: timber, sliderock, ledge, and ridge. He found goats spending 4% of their summertime in timber, 36% in sliderock, 54% in ledge, and 6% in ridge areas. In winter, goats were seen 16% of the time in timber, 70% in ledge areas, and 14% of the time on ridges. M. J. Thompson (1981) found goats in

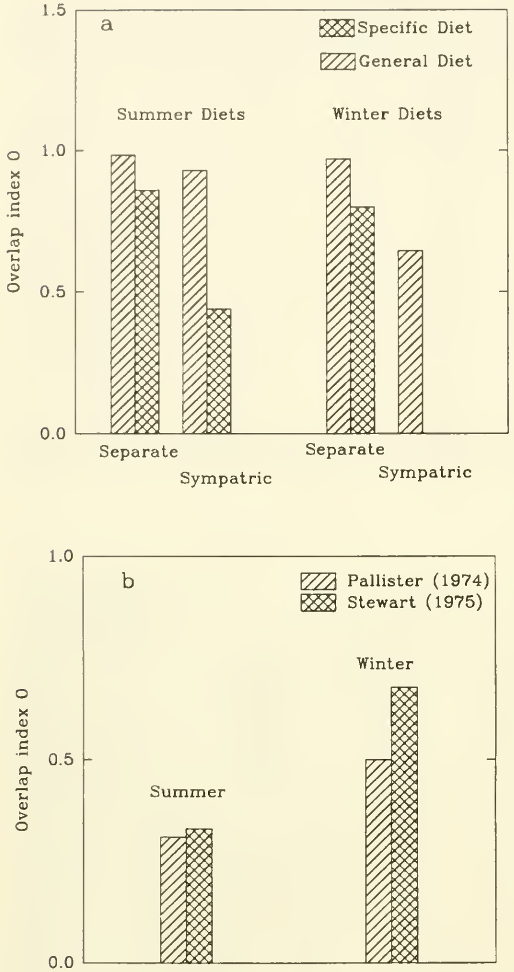

Fig. 1. Niche overlap indices for food habits (a) and habitat selection (b). Overlap indices for food are for pooled data from separate studies and data from comparative studies and are based on either general (grass, forbs, shrubs) or specific (to genera) food classifications. The index for sympatric specific summer diets is the mean of indices calculated from Pallister (1974) and Stewart (1974). The index for sympatric general summer diets is the mean from Dailey et al. (1984), Pallister (1974), and Stewart (1974). Indices for habitat selection are all from two comparative studies of sympatric sheep and goat populations.

Montana spending 90% of their summertime and 68% of their early wintertime on glacial cirques. In winter in the Bitterroot Mountains, Smith (1976) found goats 62% of the time in the "bunchgrass" association. Goats in Colorado spent 85% of their time in the substrate type described as "intermittent boulder" by R. W. Thompson (1981). Adams and Bailey (1980) classified the habitat into alpine and subalpine areas. Within the alpine community they identified tundra and rock subcomponents. Goats spent 58% of their time during winter in the tundra and 42% in rock areas. The subalpine community was subdivided into rock, shrubs, and trees. Goats were seen 35% of the time in rock areas, 10% in shrub, and 55% in tree areas. Von Elsner-Schack (1986) studied goats in Alberta and divided the study area into rock, gravel, and grass substrate types. In spring-summer, goats used the rock substrate 24%, the gravel substrate 26%, and the grass areas 50% of the time.

Few studies examined habitat use by sheep and goats simultaneously. Chadwick (1974) found some habitat segregation but did not quantify the differences. Geist (1971) found that goats in winter spent approximately 52% of their time in sheer cliff areas while sheep spent only 28% of their time in these areas. In the two Montana studies of bighorn sheep, Stewart (1975: 68, 96) and Pallister (1974: 28, 56) also recorded habitat use by goats in their study areas. Habitat use overlap indices based on Pallister's (1974) data were low for summer (0.31) and winter (0.50). The summer overlap index (0.33) from Stewart's (1975) data was similar to Pallister's value, but the winter index (0.68) was slightly higher (Fig. 1b).

Another area of potential overlap between goats and sheep is the physical characteristics of the environment. Several investigators separately quantified habitat use by goats and sheep relative to distance from escape terrain, slope, and elevation (Table 3). The average distance to escape cover in summer was significantly greater for goats ($t = 6.04$, $n = 9$, $P < .01$). Average slope used did not differ within species between winter and summer but did differ significantly between species in both seasons ($F = 15.2$, $n_1 = 7$, $n_2 = 6$, $P < .01$), with goats using steeper areas (Table 3). No difference in use was found between species or seasons for average elevation. Thus, goats preferred steeper slopes and were found further from escape terrain than were sheep.

DISCUSSION

Wildlife biologists have been implicitly using data compiled separately on resource use of goats and sheep to formulate views

TABLE 3. Means (± SE, n) of physical habitat characteristics by sheep and goats. Distance to escape habitat (DEH) values are the maximum distances at which $\geq 80\%$ of the animals were found. Values for slope and elevation are the means of data reported in the literature. An asterisk next to a measurement indicates significant ($P < .05$) differences between sheep and goats. Footnotes list references of original data.

	Summer		Winter	
	Sheep	Goats	Sheep	Goats
DEH[a]	120 ± 11.6 m, 4	305 ± 25.6 m, 5*	278 ± 103 m, 4	
Slope[b]	22 ± 2.6°, 4	41 ± 5.2°, 4*	24 ± 6.5°, 2	47 ± 8.4°, 3*
Elevation[c]	2655 ± 325.3 m, 4	2799 ± 320.8 m, 4	2431 ± 306.5 m, 4	2354 ± 376.7 m, 3

[a] Hjeljord 1971, Oldemeyer et al. 1971, Frisina 1974, Pallister 1974, McFetridge 1977, R. W. Thompson 1981, Tilton and Willard 1982, Fox 1983, Whitfield 1983, Martin 1985, Smith 1986

[b] Kuck 1973, Frisina 1974, Pallister 1974, Chadwick 1977, Smith 1976, R. W. Thompson 1981, Whitfield 1983, Martin 1985, Hayden 1989

[c] Frisina 1974, Pallister 1974, Smith 1976, Adams and Bailey 1980, M. J. Thompson 1981, R. W. Thompson 1981, Whitfield 1983, Martin 1985, Hayden 1989

concerning competition between the two species. Differences found in this review between results from separate and comparative studies indicate a danger in using data from separate studies. Food habits data from separate studies, based on general forage classes and forage species, indicated extensive overlap in goat and sheep diets. Data on habitat use from such studies also indicated goats and sheep mutually used "grass" and "tree" habitat types and similar elevations in the subalpine/alpine zones. These data strengthen the commonly held consensus of extensive resource overlap and support concerns that goats and sheep might not coexist if resources are limiting. In contrast, data from comparative studies, where specific diet composition and habitat use are considered, indicate substantial reductions in overlap when goats and sheep co-occur in an area.

Consequently, comparisons of data from separate studies might be useful in determining the amount of resource overlap that is possible between similar species but cannot be used to estimate what that overlap would be in sympatry. Only results from comparative studies of sympatric populations can be used to predict how two species will interact. Even in such comparative studies, my analysis indicates that researchers should avoid the use of general resource categories.

Currently, we have only two comparative studies of detailed resource use by goats and sheep. This is hardly a sufficient data base from which to draw valid conclusions concerning resource overlap or the potential for competition between goats and sheep. If scientifically sound conclusions about interactions between goats and sheep are to be formulated, additional comparative studies are needed. Only after such studies can we address questions concerning competition and competitive interactions between sheep and goats.

If the pattern of reduced resource overlap in sympatry withstands further study, it may be the result of resource partitioning. Whether this is the case and whether this resource partitioning is in turn a result of competitive interactions cannot be addressed with this data base. If resource partitioning is found to be a major factor in the coexistence of sympatric native goat and sheep populations, the low resource overlap found in the two comparative studies involving nonnative goats indicates goats and sheep may also exhibit such partitioning when one or the other species is an exotic introduction. However, Adams et al. (1982) cautioned that certain conditions (land development, agricultural activity, etc.) might limit selection options for one or the other species. In such cases resource partitioning may not be possible, resulting in extensive overlap of resource use between goats and sheep, possibly to the detriment of one of the species if resources are limiting.

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PREDATION OF ARTIFICIAL SAGE GROUSE NESTS IN TREATED AND UNTREATED SAGEBRUSH

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ABSTRACT.—We measured predation on 120 artificial Sage Grouse (*Centrarcus urophasianus*) nests in montane sagebrush grassland in northern Utah. We examined nests in areas that had been chained and seeded 25 years previously (treated areas) and in areas that were untreated. Predation rates of artificial nests were higher in areas of untreated sagebrush, even though these areas had greater sagebrush cover, taller shrubs, and greater horizontal plant cover. These results differ from those previously hypothesized for treated sagebrush habitat and may reflect a greater abundance of other potential prey species, especially lagomorphs, in untreated areas that attracted greater densities of predators. In addition, over 80% of nests were depredated by mammals, which hunt using olfaction and are less likely than avian predators to be affected by nest cover. We conclude that, after treated sagebrush has recovered to some degree, predation rates of Sage Grouse nests may be lower in treated sagebrush. Consequently, factors other than nest predation (e.g., winter food, thermal cover, insects, perennial forb abundance) may be more important reasons for preserving mature sagebrush stands for Sage Grouse.

Key words: Sage Grouse, Centrarcus urophasianus, *sagebrush, nest, predation, habitat.*

A key problem in the conservation of wildlife species is fragmentation of large contiguous areas of preferred habitat (Lovejoy et al. 1984, Wilcove 1985, Yahner and Scott 1988), a problem that has plagued the management of upland game bird populations in western North America (Vale 1974, Braun et al. 1977). In particular, Sage Grouse populations have declined in some areas, apparently in response to widespread treatment (chaining, spraying, burning, etc.) of sagebrush-dominated rangeland to benefit livestock production (Schneegas 1967, Klebenow 1970, Braun et al. 1977). However, few studies have examined whether such treated areas can recover to become suitable Sage Grouse habitat.

Sagebrush treatment may reduce Sage Grouse populations by eliminating mature shrubs, which may be important in protecting nests from visual predators (Dalke et al. 1963, Braun et al. 1977, Autenrieth 1981, Connelly et al. 1991). In addition, treated areas planted to grass cover (e.g., crested wheatgrass, *Agropyron desertorum*) often recover shrubs slowly (Vale 1974, MacMahon 1987). Sagebrush treatment may therefore permanently reduce nesting cover.

For ground-nesting birds in general, dense shrub cover may not always be beneficial; it may increase nest predation by supporting greater populations of alternate prey and attracting greater densities or attention of predators (Croze 1970, Duebbert and Kantrud 1974, Taylor 1977, 1984). Alternate prey, however, may sometimes decrease nest predation by diverting predator effort during nest incubation (Byers 1974, Weller 1979, Crabtree and Wolfe 1988). For areas recovering from sagebrush treatment that have relatively low shrub cover, it is not clear whether Sage Grouse nest predation is greater than in untreated areas with greater cover.

In this study we tested the hypothesis that artificial Sage Grouse suffer higher predation rates in treated than in untreated sagebrush. We also measured vegetation characteristics associated with nest sites to determine which habitat components might contribute to nest predation. Finally, we measured indices of lagomorph, small mammal, and predator abundance within treated and untreated areas to establish whether higher nest predation rates were associated with a higher density of alternate prey and/or predators.

STUDY AREA

The study was conducted on the property of Deseret Land and Livestock, an 80,000-ha ranch located in northwestern Utah along the

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Wyoming border (Rich County). We conducted the study on mid-elevation (2000 m) benches dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), rabbitbrush (*Chrysothamnus viscidiflorus*), and several herbaceous species, mainly western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Stipa comata*), Indian ricegrass (*Oryzopsis hymenoides*), bluegrass (*Poa sandbergi*), and *Phlox* spp.

Many separate 1000–5000-ha pastures, totalling nearly 40% of the 32,000 ha of mid-elevation sagebrush grassland on the ranch, were treated by discing or spraying between 1960 and 1965, resulting in a partial loss of sagebrush. These treated areas were seeded with crested wheatgrass (*Agropyron desertorum*) to improve forage for livestock. Thus, two distinct habitats exist on the study area: untreated areas with 5–20% herbaceous cover and 10–40% shrub cover (mostly sagebrush), and treated areas with 5–40% herbaceous cover (mostly crested wheatgrass) and 0–20% shrub cover (mostly sagebrush and rabbitbrush). Treated areas typically had recovered some shrub cover, but shrubs were shorter and less dense than in untreated areas.

Alternate prey for potential Sage Grouse nest predators included lagomorphs (white-tailed jackrabbits [*Lepus townsendi*], mountain cottontails [*Sylvilagus nuttalli*], and pygmy rabbits [*Brachylagus idahoensis*]) and small mammals (*Peromyscus maniculatus* and *Perognathus parvus*). The primary mammalian nest predators were coyotes (*Canis latrans*), badgers (*Taxidea taxus*), and chipmunks (*Eutamias minimus*). Principal avian nest predators were Common Ravens (*Corvus corax*), Black-billed Magpies (*Pica pica*), and California Gulls (*Larus californicus*) (all Sage Grouse leks [breeding grounds] in the study area were within 10 km of a large gull colony on Neponset Reservoir).

METHODS

Artificial Nests

Predation rates of artificial nests were measured in each habitat type during the Sage Grouse nesting season of 1991. We set up artificial nests at 160-m intervals along three 1.6-km transects radiating at random compass bearings and commencing 0.8 km from each of four Sage Grouse leks (two in each habitat type). These locations represented the area most likely used for nesting by females attending each lek (Wallestad and Pyrah 1974, Beck 1977). Thus, we used a total of 120 nests, with 10 nests per transect, 3 transects per lek, and 2 leks per habitat type. To achieve some level of replication, we selected 2 leks in each habitat type so that sampling areas delineated by a 2.2-km radius surrounding each lek did not overlap and included different groups of pastures. Leks in treated areas were located in pasture complexes treated in different years and separated by untreated sagebrush.

We drove along each transect in a vehicle to avoid leaving a scent trail. At each 160-m interval, we placed artificial nests under the closest shrub (>10 cm height) to a point at a random distance (10–30 m) along a line perpendicular (randomly left or right) to the main transect. These precautions were taken to reduce the chance that avian predators could "cue" on artifical nests by following tire marks along the main transect (Galbraith 1987, MacIvor et al. 1990) and the chance that mammalian predators could detect nests by following human scent. However, either type of predator could have followed tracks left by the vehicle.

Each "nest" consisted of three unmarked brown chicken eggs. Nests were placed in the field between 30 April and 3 May 1991 during the Sage Grouse nesting period at Deseret Ranch. Nests were checked 15 days later and were considered depredated if all eggs were destroyed or missing, or partially depredated if one or two eggs remained. We attempted to identify the nest predator as either mammalian or avian, based on characteristics of egg remains (Rearden 1951, Patterson 1952). We could identify likely predators at 43 of 57 depredated nests.

Habitat Characteristics

We measured vegetation characteristics, alternate prey abundance, and badger abundance at or near artificial nest transects to evaluate potential differences among habitat types. We measured vegetation characteristics when artificial nests were checked for predation. Specifically, we estimated percent cover of shrubs and herbaceous plants as well as height of the tallest shrub in four Daubenmire (1968) plots at each nest site. These plots were spaced 5 m apart along a 20-m transect extending from the nest site and parallel to the main artificial nest transect. We measured horizontal cover by counting the number of 5 × 5-cm squares on a 45 × 45-cm board that were obscured by the nest bush to a viewer at 10 m distance and 40 cm height (Jones 1968, Klott and Lindzey 1990).

Abundance of alternate prey for potential predators was estimated in July 1991 in both sagebrush habitat types within 1 km of the artificial nest transects. We estimated lagomorph abundance by counting the number of lagomorph fecal pellets in ten 2 × 2-m plots located every 15 m along 150-m transects. We counted fecal pellets along four randomly located transects in each habitat type. We estimated abundance of small mammals by establishing two replicate 200 × 200-m grids of 25 Sherman® live traps placed 50 m apart in each habitat type. Traps were baited with rolled oats and peanut butter and checked for 3 nights (11–13 July).

We estimated abundance of badgers, a principal mammalian nest predator, by counting the number of active badger holes seen along 2.5-km transects in mid-July 1991. Nine transects were randomly located within 1 km of artificial nest sites in each habitat type. Active badger holes were identified by fresh digging, a large oval hole, and presence of scat and/or tracks.

Statistical Tests

Proportions of nests depredated were compared with chi-square tests for treated vs. untreated areas and with Fisher's Exact Test for mammalian vs. avian predators. We compared the mean proportion of depredated nests and vegetation characteristics in treated vs. untreated areas with a nested ANOVA (Dowdy and Wearden 1991) with leks as experimental units and transects as subsamples. All proportions were arcsine–square root transformed for statistical tests to equalize variance of proportions (Neter and Wasserman 1974). Because there were only two replicate leks in each habitat type, the design had a low power to detect differences (Neter and Wasserman 1974). Consequently, we selected an alpha of .10 for significance tests in the nested ANOVA.

We compared the abundance of lagomorphs, small mammals, and badgers between habitat types using *t* tests. Each walked transect was considered a subsample of badger abundance within each habitat type. The relationship between different vegetation characteristics and nest success was analyzed for two sampling units, transect and nest, that measured habitat characteristics at different scales. With transects as sampling units, the relationship between mean vegetation characteristics and proportion of nests depredated on each transect was tested using multiple linear regression and partial correlation. With nests as sampling units, the relationship between vegetation characteristics and nest success at individual nest sites was tested with multiple logistic regression. All statistical tests were performed using NCSS (Number Cruncher® Statistical System).

RESULTS

Female grouse attended leks (8–20 males/lek) and nested in both treated and untreated sagebrush. Of 22 hens radio-collared on wintering areas between 1985 and 1989, 9 nested in treated areas the following spring (R. Danvir unpublished data). This frequency (40.9%) was not significantly different from the proportion of sagebrush grassland on the ranch that had been treated (40%) ($X^2 = .009$, df = 1, $P > .90$).

Overall, artificial nests were depredated significantly less frequently in treated sagebrush (10 of 60) than in untreated sagebrush (33 of 60) ($X^2 = 19.5$, df = 1, $P < .001$). Mean proportion of nests depredated was greater in untreated than in treated sagebrush and the difference approached significance ($F = 6.3$, df = 1,2, $P = .12$; Table 1). Mean proportion of nests depredated differed significantly among leks ($F = 4.6$, df = 2,8, $P = .04$; Table 2). The majority of nests were depredated by mammals (37 of 43), with birds accounting for the remaining 6. The proportion of nests depredated by mammals did not differ significantly among habitat types (treated: 9 of 11; untreated: 28 of 32, Fisher's Exact, $P = .63$).

Differences in nest predation among habitat types and leks were attributed to differences in vegetation characteristics (Table 1, 2). Horizontal cover (% of cover board obscured) and maximum shrub height were significantly greater in untreated areas, but shrub and herbaceous cover were not (Table 1). Leks varied significantly in horizontal cover, herbaceous cover,

TABLE 1. Artificial nests depredated (%) and habitat characteristics for treated and untreated areas of sagebrush grassland at Deseret Ranch.

	Untreated habitat			Treated habitat			
Variable	$\bar{x}$	SE	*N*	$\bar{x}$	SE	*N*	*P*[a]
Nests depredated (%)	55.0	16.2	2	16.7	14.3	2	.12
Vegetation characteristics							
Horizontal cover (%)	89.3	2.5	2	69.4	2.4	2	.08
Shrub cover (%)	27.0	1.8	2	17.0	1.7	2	.15
Herbaceous cover (%)	21.1	1.6	2	18.2	1.4	2	.51
Maximum shrub height (cm)	65.0	3.1	2	36.1	2.8	2	.06
Alternate prey abundance							
Lagomorph pellets (#/m^2)[b]	17.0	3.5	4	2.5	3.6	4	.006
Small mammals (#/100 trap-nights)	8.6	0.8	2	12.6	0.8	2	.02
Predator abundance							
Badger holes (#/km)	2.0	0.52	9	0.67	0.19	9	.02

[a] For nests depredated and vegetation characteristics, nested ANOVA, $P < .10$ significant, see text; for alternate prey abundance, *t* tests, $P < .05$ significant.
[b] Data were log-transformed to account for nonnormal distributions.

TABLE 2. Mean proportion of nests depredated and vegetation characteristics (±SE, $N = 3$) associated with Sage Grouse leks in treated and untreated sagebrush.

	Lek				
	Untreated habitat		Treated habitat		
Variable	Dip	Kate Hollow	Neponset	Alkali Hollow	*P*[a]
Nests depredated (%)	66.7 ± 14.5	43.3 ± 5.8	6.7 ± 6.7	26.6 ± 12.0	.04
Horizontal cover (%)	89.3 ± 2.2	87.6 ± 5.4	65.3 ± 5.3	75.6 ± 2.8	.09
Shrub cover (%)	24.3 ± 2.9	29.0 ± 0.7	19.3 ± 3.6	16.0 ± 4.9	.22
Herbaceous cover (%)	26.0 ± 3.2	17.0 ± 0.7	17.6 ± 0.4	15.7 ± 4.0	.07
Maximum shrub height (cm)	70.7 ± 3.3	59.9 ± 4.9	33.4 ± 5.6	37.5 ± 5.5	.005

[a] From nested ANOVA, $P < .10$ significant, see text.

and maximum shrub height (Table 2). With transects as sampling units, we regressed proportion of nests depredated along the transect against the transect mean of each of the habitat variables (Fig. 1). Nest predation increased significantly with each variable except shrub cover. Each variable was correlated with each of the others, so we examined the independent effects of each variable by calculating its partial correlation coefficient (Table 3; Neter and Wasserman 1974). Horizontal cover had a significant positive partial correlation with nest depredation rate, while shrub cover had a significant negative partial correlation. Herbaceous cover showed a positive partial correlation with nest predation that was nearly significant ($P = .12$), but maximum shrub height showed nearly zero partial correlation with nest predation. Overall, vegetation characteristics measured with transects as sampling units explained 86% of the variation in nest predation.

With nest sites as sampling units, we used logistic regression to analyze the relationship

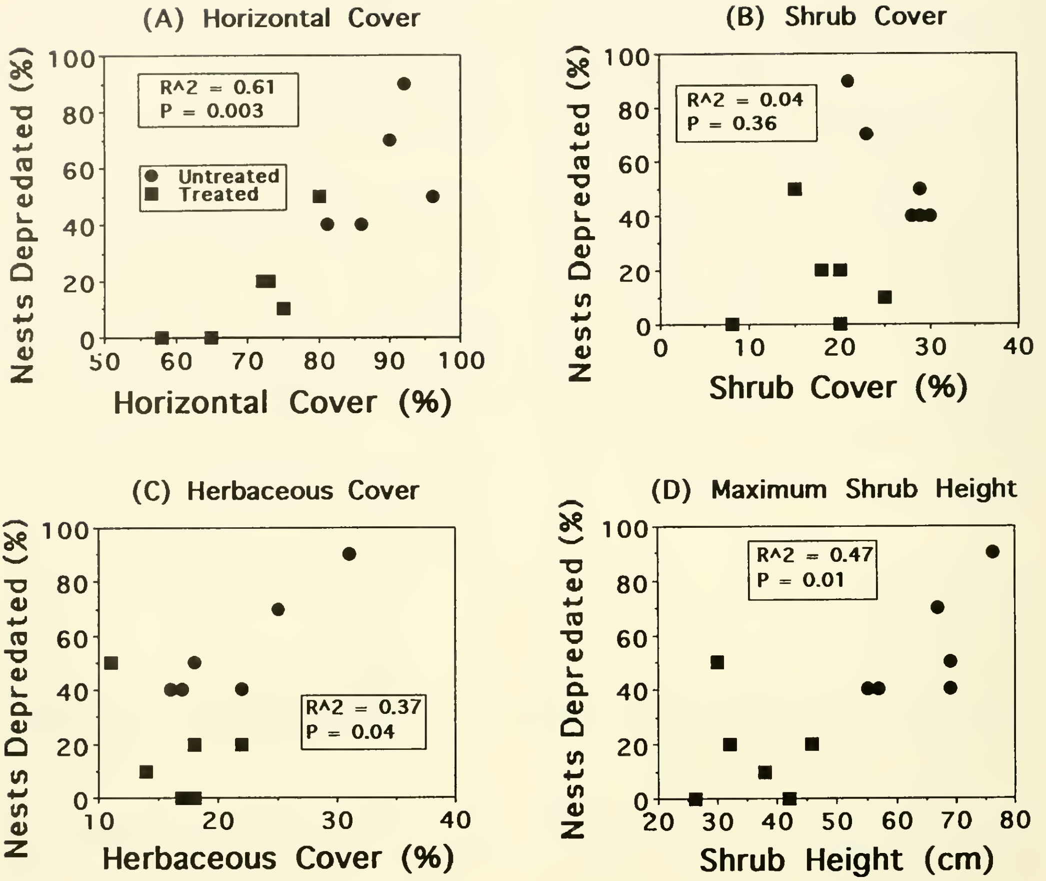

Fig. 1. Relationships of proportion of nests depredated (%) and four vegetation characteristics (see text for precise definitions): (A) horizontal cover, (B) maximum shrub height, (C) shrub cover, and (D) herbaceous cover. R^2 values are for linear regressions. Data points represent transect means, presented separately for treated areas (●) and untreated areas (■).

between the success (no predation) of individual nests and vegetation characteristics associated with each nest site (Table 4). As was found with transect sampling units, nest predation increased with increasing horizontal cover, herbaceous cover, and maximum shrub height, but not shrub cover. With all four variables considered simultaneously (multiple logistic regression), however, only horizontal cover and maximum shrub height were significant. Overall, vegetation characteristics at nest sites explained only 12% of the variation in nest predation.

Abundance of lagomorphs was significantly greater in untreated areas, but abundance of small mammals (primarily *Peromyscus maniculatus*) was greater on treated areas (Table 1). Fresh badger holes, however, were significantly more common in untreated areas. Consequently, greater predation of artificial Sage Grouse nests appeared to be associated with higher abundances of lagomorphs and badgers, but lower numbers of small mammals.

DISCUSSION

Predation rates of artificial nests were higher in untreated sagebrush in spite of greater nest cover. These results contrast with those from studies that found greater predation rates on nests in sparser cover (Wallestad and Pyrah 1974, Connelly et al. 1991). However, Autenrieth (1981) found similar results to ours, namely lower predation rates on nests

TABLE 3. Simple and partial correlation coefficients ($N = 12$) of proportion of nests depredated with four vegetation characteristics when all four variables are included in a multiple regression analysis.

Variable	Simple r[a]	Partial r	P[b]
Horizontal cover	.78	.89	.0004
Shrub cover	.20	−.75	.01
Herbaceous cover	.61	.52	.12
Maximum shrub height	.69	−.04	.90

[a] For P values, see Figure 1.
[b] P value for the partial correlation coefficient.

in a crested wheatgrass planting with sparse (<5%) sagebrush cover than in untreated sagebrush. In addition, Patterson (1952) found higher nest predation rates under taller, denser sagebrush.

At least two patterns emerge that may explain the conflicting results of these studies. First, nest predation was higher when predator densities were higher, regardless of nest cover (Autenrieth 1981, Angelstam 1986, this study). Badgers were the most frequent large mammalian nest predator (Patterson 1952, this study) and were more abundant in untreated areas. Second, nest cover seems to be more important in protecting nests from visually hunting predators, such as ravens, magpies, or gulls (Jones and Hungerford 1972, Picozzi 1975, Autenrieth 1981, Yahner et al. 1989, Sullivan and Dinsmore 1990), than those hunting by olfaction, such as badgers, coyotes, or chipmunks. These two patterns suggest that the type and density of predators may affect the degree to which nest cover reduces nest predation (Bowman and Harris 1980, Angelstam 1986).

An additional factor that may explain discrepancies among studies is the fact that our treated areas were >25 years old and had recovered some sagebrush. Wallestad and Pyrah (1974) and Connelly et al. (1991) studied areas that had been recently treated and perhaps still contained pretreatment densities of predators. In this study predator densities would have had plenty of time to decline following sagebrush treatment. Thus, the effect of habitat on nest predation may be due primarily to the densities of predators supported by the habitat.

Our conclusions are based on artificial nests; several studies have shown that the fate of artificial nests may not reflect that of natural nests (Angelstam 1986, Storaas 1988, Yahner and Voytko 1989). However, fates of artificial nests are likely to reflect differences in predation rates among habitats and are legitimate tools for testing the hypotheses in this paper.

Vegetation characteristics associated with increased nest predation depended on the sampling unit used in the analysis. When transects were used as sampling units, increased nest predation was associated with increased horizontal and herbaceous cover (Fig. 1, Table 3). When individual nest sites were used, horizontal cover and maximum shrub height were the only significant factors (Table 4). Moreover, vegetation characteristics averaged for a transect explained considerably more variance in nest predation (86%) than did characteristics associated with individual nest sites (12%). Thus, the effect of vegetation characteristics on nest predation may depend on the scale at which they are measured (Bowman and Harris 1980, Allen and Starr 1982). In this case, vegetation characteristics of the overall habitat in which nest sites are located (transect scale) may be more important than characteristics directly at nest sites.

The correlation between horizontal and herbaceous cover and increased nest predation at the transect scale may actually reflect an indirect effect of habitat on nest predation rate: greater horizontal and herbaceous plant cover may be preferred by lagomorphs and other small mammals, which may then attract a greater density of predators. A greater density

TABLE 4. Results of multiple logistic regression of nest predation (0 = nest destroyed, 1 = no predation) vs. vegetation characteristics at individual nest sites.

Variable	Coefficient	SE	Variance explained (%)	P[a]
Horizontal cover (%)	−0.024	0.012	6.1	.04
Shrub cover (%)	0.010	0.020	0.2	.62
Herbaceous cover (%)	−0.009	0.021	0.2	.65
Maximum shrub height (cm)	−0.021	0.009	6.4	.03

[a] From x^2 test within multiple logistic regression, $P < .05$ significant.

of predators may then inflict a greater predation rate on Sage Grouse nests. Our data are somewhat consistent with this hypothesis, in that lagomorphs and badgers were more abundant in untreated areas, and badger holes were often associated with burrow systems used by cottontails and pygmy rabbits. However, small mammals, which provide a lower prey biomass than lagomorphs, were more abundant in treated areas. Nevertheless, the association between vegetation, alternate prey abundance, predator density, and nest predation rates appears to be the most likely hypothesis explaining our results.

At the scale of transects, nest predation rate significantly decreased with increasing shrub cover, given horizontal and herbaceous cover (Table 3). However, this pattern was not observed at the scale of individual nest sites (Table 4). Nevertheless, shrub height was important for explaining nest predation at individual nest sites. Shrub cover and height are thought to be most important in preventing predation by visually hunting predators such as birds (Jones and Hungerford 1972, Picozzi 1975, Autenrieth 1981) rather than mammals that hunt by olfaction (Angelstam 1986, Storaas 1988). However, our data suggest that increasing shrub cover and height may also help reduce mammalian nest predation. Thus, for a given predator density, increased shrub cover and height may reduce Sage Grouse nest predation (Wallestad and Pyrah 1974, Autenrieth 1981, Connelly et al. 1991).

CONCLUSIONS

Our results suggest that lower nest predation rates for Sage Grouse may occur in recovering treated sagebrush because the sagebrush treatment reduces the long-term density of predators. This result conflicts with the commonly accepted idea (Lovejoy et al. 1984, Wilcove 1985) that habitat fragmentation always increases predation of bird nests. There is little doubt that sagebrush treatment significantly reduces Sage Grouse populations in both the short and long term (Dalke et al. 1963, Braun et al. 1977, Autenrieth 1981). However, the claim that sagebrush treatment increases nest predation rates (Braun et al. 1977, Connelly et al. 1991) is probably not the best reason for preserving contiguous stands of mature big sagebrush. Treating sagebrush may reduce Sage Grouse populations in the long term for reasons other than nest predation (Braun et al. 1977), including elimination of winter habitat (Homer 1990), removal of year-round thermal cover (Moen 1973, Autenrieth 1981), and reduction of perennial forbs, an important food for hens and chicks (Autenrieth 1981). Consequently, recommendations to preserve mature sagebrush habitats should probably be made on the basis of these factors rather than nest predation.

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TIMING, DISTRIBUTION, AND ABUNDANCE OF KOKANEES SPAWNING IN A LAKE TAHOE TRIBUTARY

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ABSTRACT.—We counted kokanee spawners and carcasses every 1–7 days from mid-September through mid-November in 1991 and 1992 in Taylor Creek, a tributary to Lake Tahoe, California-Nevada. Less than 1% of the spawning run entered Taylor Creek before flow from Fallen Leaf Lake was increased on 2 October 1991; in 1992 the peak occurred on 30 September or 1 October after flows increased on 29 September. In both years spawners concentrated in the middle three of five stream reaches below the impassable Fallen Leaf Lake dam. From tag-and-recovery experiments, the average longevity of male spawners in the stream was 3.5 days in 1991 and 2.8 days in 1992, whereas the average female longevity was 2.0 days in 1991 and 2.3 days in 1992. Observed carcasses accounted for less than 10% of spawners counted, suggesting removal by scavengers or high predation on prespawners. An estimated 1928 males and 1309 females spawned in 1991, and 8021 males and 8712 females spawned in 1992. Our estimate of 3237 spawners in 1991 compared favorably to our estimate of 3520 ± 1474 prespawners staging in Lake Tahoe in mid-September. An index of kokanee abundance in Lake Tahoe has historically been based on 1-day surveys every 1 November since 1960; however, estimated total spawner abundance was 19 times higher than the annual index of 158 spawners in 1991, and 141 times higher than the index count of 100 spawners in 1992. The index count and mean fork lengths of spawners (278 ± 10 mm [2 SE] for males, and 248 ± 3 mm for females) in 1991 and 1992 were the lowest on record.

Key words: kokanee, spawner, abundance, life span, turnover rate.

Kokanee salmon (*Oncorhynchus nerka*) represent an important food source for lake trout (*Salvelinus namaycush*) (Frantz and Cordone 1970) and overwintering Bald Eagles (*Haliaeetus leucocephalus*) (U.S. Forest Service [USFS] 1979), are important zooplanktivores, and provide a valuable sport fishery in Lake Tahoe (Cordone et al. 1971). Despite these prominent recreational and ecological roles, little is known of the survival or abundance of this population. The long-term record consists of 1-day spawner surveys of Taylor Creek on or near 1 November every year, and this has served as an index of abundance. Population trends have been inferred from these data, but the relationship of this index to actual abundance has not been evaluated. Interannual differences in run-timing could violate the critical assumption that these annual spawner counts represent some constant, but unknown, fraction of the total run size. Therefore, the purpose of this study was to estimate absolute abundance of spawners, compare annual 1 November index counts to absolute abundance estimates, and determine whether index counts represented a constant fraction of the total spawning population among years. If the index count proves inadequate, then some improved, but streamlined, monitoring program should replace it. Therefore we also examined whether, over the spawning season in Taylor Creek, changes occurred in the sex ratio or distribution of spawners among reaches. Temporal changes in either of these could bias population estimates and must be accounted for in the design of future kokanee spawning surveys.

STUDY SITE

Kokanees were originally introduced into the lake in 1944, but the population remained small until 1960 when a popular summer sport fishery emerged (Cordone et al. 1971). Most natural reproduction occurs in Taylor Creek, but the population has also been supplemented irregularly by stocking fry into the creek or fingerlings into various regions of the lake

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(T. Frantz personal communication). Kokanees spawn and die in Taylor Creek in autumn. The eggs and alevins incubate in gravel redds until spring, emerge and migrate to Lake Tahoe, then reside in the lake 3–4 years before spawning in the natal stream. Although annual discharge from Taylor Creek ranks only fourth among the lake tributaries (Byron and Goldman 1989, USFS unpublished data), kokanees spawn there because elevated autumn flows have been maintained since 1959. USFS generally increases flow from the dam on Fallen Leaf Lake (Fig. 1) in early October "to protect and enhance the habitat for fish . . . to insure an adequate and increasing food supply for wintering eagles" (USFS 1979). In general, flows remain low during summer but are increased during the first week in October to provide adequate flows during spawning and incubation periods. Additional spawning occurs along the western and eastern shorelines and in several other tributaries, but these represent a small fraction of the total kokanee population (Cordone et al. 1971, B. Allen unpublished data).

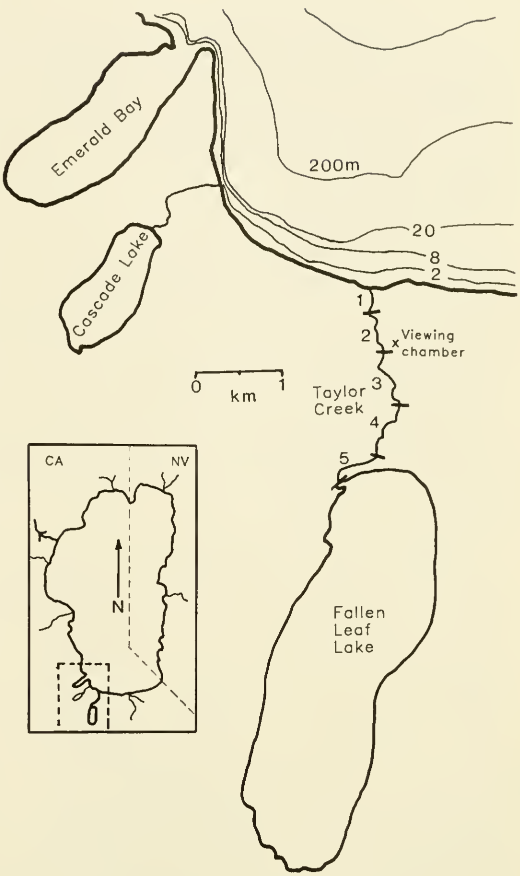

Fig. 1. Map of southwestern Lake Tahoe (the dashed box inside the inset), showing lake bathymetry near Taylor and Cascade creeks, California. Locations of stream sections in Taylor Creek between Fallen Leaf Lake and Lake Tahoe during the 1991 spawning season are numbered. The viewing chamber at the USFS Interpretive Center, Cascade Lake, and Emerald Bay are indicated.

Taylor Creek flows 2.6 km from a controlled dam on Fallen Leaf Lake through a forested valley into the southwest corner of Lake Tahoe (Fig. 1). We divided the stream into five survey sections, based on gradient differences, between the mouth and base of the dam to determine spatial distribution of kokanees during the spawning season (Table 1, Fig. 1). From the mouth of Taylor Creek, the lake bottom slopes gradually to 6 m deep about 0.4 km offshore, then drops steeply to 30 m deep approximately 0.6 km offshore. The lake bottom is much steeper near the mouth of Cascade Creek (deeper than 60 m within 100 m of shore) approximately 2.2 km northwest of Taylor Creek (Fig. 1). During the 1991 and 1992 spawning seasons, the lake level was 2 m lower than normal and 0.3 m below its natural rim due to six years of drought; this did not block spawners' access into the stream.

METHODS

We monitored the relative abundance of kokanees staging offshore in Lake Tahoe prior to and during the spawning season using scuba surveys, echosounding, and underwater video with a remotely operated vehicle (ROV; see Beauchamp et al. 1992). We searched the lake from shore to 30 m deep for the 2.2 km between Taylor and Cascade creeks, and the area within a 200-m radius of the creek mouths (Fig. 1). Although we infrequently searched other streams and shoreline areas reported to have spawning activity in past years, we found no spawners or carcasses in either year. A school of adult kokanee was videotaped offshore Cascade Creek on 12 September 1991. The tape was later rerun as a series of freeze frames. Each frame was divided into 16 vertical strips (25 mm wide by 295 mm long), marked on the monitor, and kokanees were counted within each strip. Each frame sampled different segments of the school. The school was further stratified into low- and high-density regions, and mean density and standard deviation of kokanees were estimated from the strips in each region; mean densities were then multiplied by the total number of low- and high-density strips, and products were summed to estimate the total number in the school.

In 1991 we surveyed all reaches of Taylor Creek weekly from 17 September to 19 November, recording the number of salmon in each section that were alive or dead, male or female. A weir, installed 40 m upstream of the lake on 16 October 1991 to capture spawners, was opened 2 days later because of low catches. It was closed again on 28 October, and in one night it trapped sufficient spawners for tagging in a tag-and-recover estimate of longevity in the stream.

In 1992 USFS personnel first reported spawners in Taylor Creek on 24 September. Tahoe Research Group or USFS personnel counted spawners in sections 1 and 2 twice during the first week of the spawning run. Since counts in section 2 represented at least half the spawners during the early part of the run, we doubled these counts to approximate total number of spawners in the stream on days of the counts. We surveyed all reaches of Taylor Creek either daily or every other day from 1 October to 4 November. Numbers of spawners during intervening days were estimated by linear interpolation.

To estimate the total spawning escapement of males and females into Taylor Creek, we used the relationship:

$$N_j = \frac{\sum_{i=1}^{T} N_{ij}}{D_j}$$

where N_j = total abundance of sex j, N_{ij} = number of sex j spawners counted (or interpolated) on day i, T is the total number of days in the spawning season, and D_j is the average gender-specific longevity (in days) after entering the stream.

We estimated average gender-specific longevity, D_j, under controlled and natural conditions. First, five males and five females were trapped at the mouth of Taylor Creek overnight on 28–29 October 1991, tagged with orange dart tags, and released into the stream profile viewing chamber at the USFS Interpretive Center (Fig. 1). USFS personnel also moved additional untagged kokanee salmon into the viewing chamber periodically. By observing behavior, relative health, and mortality of tagged and untagged spawners in the viewing chamber, we concluded that tags had no apparent detrimental effect, and no tags were lost. We surveyed the stream and chamber every 1–3 days until all tagged fish had died. We obtained a second estimate of longevity using the same procedure on untagged spawners in the chamber during two periods when distinct groups of spawners could be tracked over time. Finally, to estimate average longevity in the stream, we tagged and released 38 males and 21 females upstream of the weir at dusk on 29 October 1991. High winds and dense floating leaf litter prevented an adequate survey in the stream on the day after the tag release; few tagged fish remained in the stream when conditions finally permitted a survey 2 days later.

TABLE 1. Lengths and gradients of the stream sections surveyed for spawning kokanee salmon in Taylor Creek, the major spawning tributary to Lake Tahoe, California-Nevada (estimated from USGS 7.5 minute topographic map).

Section	Length (m)	Gradient
1	290	0.3%
2	550	0.9%
3	660	3.0%
4	660	1.9%
5	620	1.0%

We repeated the tagging experiment in Taylor Creek in 1992. Thirty-nine females and 5 males were captured overnight in a fyke net set at the mouth of the stream on 15 October. Each fish was anesthetized with MS-222, sexed, weighed, measured, and given two tags on the right side below the posterior insertion of the dorsal fin. Fish were allowed 8 h to recover, then were released upstream. One male died during the holding period, and 2 females were eaten by gulls (species unknown) before they could swim to cover upstream. Thus, 4 males and 37 females remained. The remaining fish were counted in the stream on 16–19, 22–23, 25, 27, 29, and 30 October. A male and female each lost one of their two tags while still alive in the stream.

Average longevity, D_j, for each study group was computed using time-density (both years) and regression (1991 only) approaches. In the time-density estimate, the number of live spawners from each group was counted on every survey day until all were dead. We estimated counts between survey dates by linear interpolation. For each sex, daily counts were summed (total spawner days) and divided by the initial number released to estimate the average number of days D_j individuals survived in the stream. Regressions were computed for the percentage of tagged males and females (and the two untagged groups in the viewing chamber) surviving as a function of time. The resulting equations were solved for number of days until survival equaled 50% to estimate D_j.

RESULTS

In 1991 kokanees staged in one large prespawning aggregation off the mouth of Cascade Creek. The creek is inaccessible to spawners due to an extremely high gradient and low autumn flows. The aggregation concentrated in a dense, 2–3-m-high band 3–10 m offshore from where the metalimnion (28–33 m deep in 10–11°C) intersects the steeply sloping lake bottom. From video samples we estimated that the aggregation contained 3520 ± 1474 (mean ± SD) mature (red-colored) kokanees. No other aggregations were found closer to Taylor Creek at any time throughout the season.

In 1991 only 8–29 spawners were counted per day in Taylor Creek during the last two weeks of September; the major portion of the run began after stream flows were increased (from 4 cfs to 8–9 cfs) on 2 October, peaked at 600 spawners on 14 October, and declined until only 14 live fish remained on 12 November (Fig. 2). All spawners and carcasses disappeared between 14 October and 18 October, 2 days after the weir was installed, but daily counts exceeded 400 spawners in the descending limb of the run after upstream access was reinstated on 18 October (Fig. 3).

The run was larger and peaked earlier in 1992 (Fig. 2). The largest number of spawners was counted on 1 October. We might have missed the actual peak, but spawner counts in section 2 on 27 and 29 September were 50–75% smaller than on 1 October. Maximum densities probably occurred on 30 September or 1 October, and sensitivity analysis of likely alternatives indicated that errors would at most increase our abundance estimate by only 1000 fish (a 6% underestimate).

Stream sections 2, 3, and 4 were the most heavily used reaches both years, whereas section 1 was lightly occupied (Fig. 3). No fish were ever seen in section 5 in 1991, but nearly 100 spawners were counted there throughout the 1992 season (Fig. 3). Proportional allocation of spawners among sections was relatively constant during both years. Temporal distribution of live and dead fish indicated little or no spawning in section 1. Only live males and carcasses of both sexes were found there, mostly during the first half of the run (Fig. 3).

Since kokanees die after spawning, live fish should be replaced by an equal number of carcasses, but carcass counts could account for only 5–10% of the number expected from declines in daily spawner counts. In three surveys divers found only 3–17 carcasses on the lake bottom within 200 m of the creek mouth. Few carcasses were washed down to the weir in 1991. Thus, emigration of spawned-out fish and flushing of carcasses could not account for the discrepancy between declining spawner counts and carcasses.

Male kokanees lived longer in the stream than females (Table 2). Consequently, males would appear more abundant because of accumulation over a longer period. In 1991 one tagged male lived in the stream for 14 days, whereas none of 21 tagged females remained after the first 3 days. Since we did not know when females disappeared over that 3-day period, we assumed a conservative linear decline to zero on the third day. In 1991, counts and linear interpolations summed to 132.0 total spawner days for the 38 tagged males; thus, males lived an average 3.5 days in the stream (Table 2). Similar analyses yielded longevity estimates of 2.0 days per female in 1991, 2.3 days per female in 1992, and 2.8 days per male in 1992 (Table 2).

Longevity estimates differed between sexes and among groups in the viewing chamber and stream in 1991. Exponential regressions of survival as a function of time in the chamber were significant for tagged males ($r = .917$, $P < .05$), untagged males ($r = .918$, $P < .05$), tagged females ($r = .867$, $P < .05$), and untagged females ($r = .972$, $P < .05$). Resulting longevity estimates were 8.3 days for tagged males, 7.5 days for tagged females, 4.4 days for untagged males, and 3.3 days for

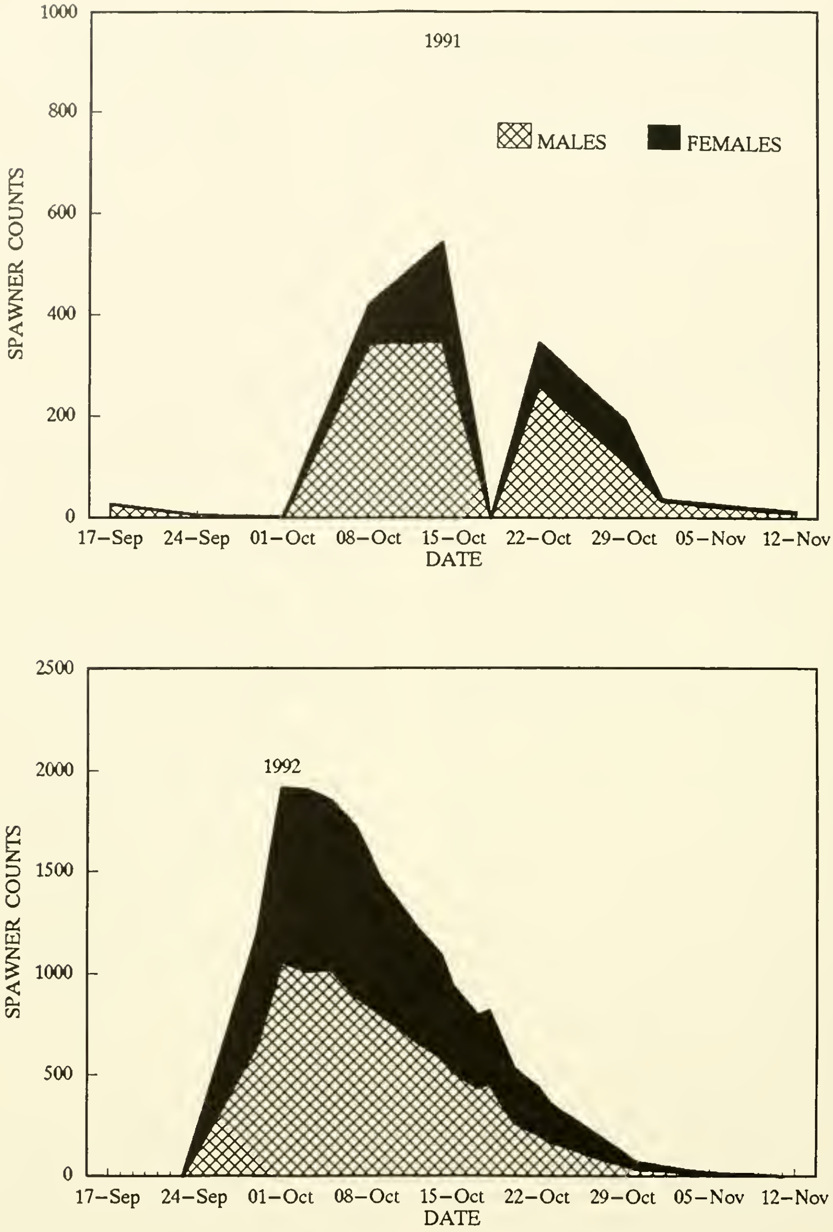

Fig. 2. Daily abundance of male and female spawners in Taylor Creek, California, in 1991 and 1992. A weir installed on 16 October 1991 prevented upstream passage from Lake Tahoe for 2 days (16-18 October).

untagged females. However, these longevities were not consistent with the rapid disappearance of spawners between 14 and 18 October, following closure of the weir on 16 October (Fig. 2), suggesting that longevity was shorter than indicated by the chamber survival experiment. In contrast to spawners in the stream, tagged and untagged fish in the chamber were passive, rarely displaying spawning or aggressive behavior. Using the exponential model for tagged males released upstream in 1991 ($r = .831$, $P < .10$) resulted in an average longevity of 3.0 days, compared to the time-density estimate of 3.5 days in Table 2. Although the exponential model accounted for 69% of the variability in survival over time, it was not

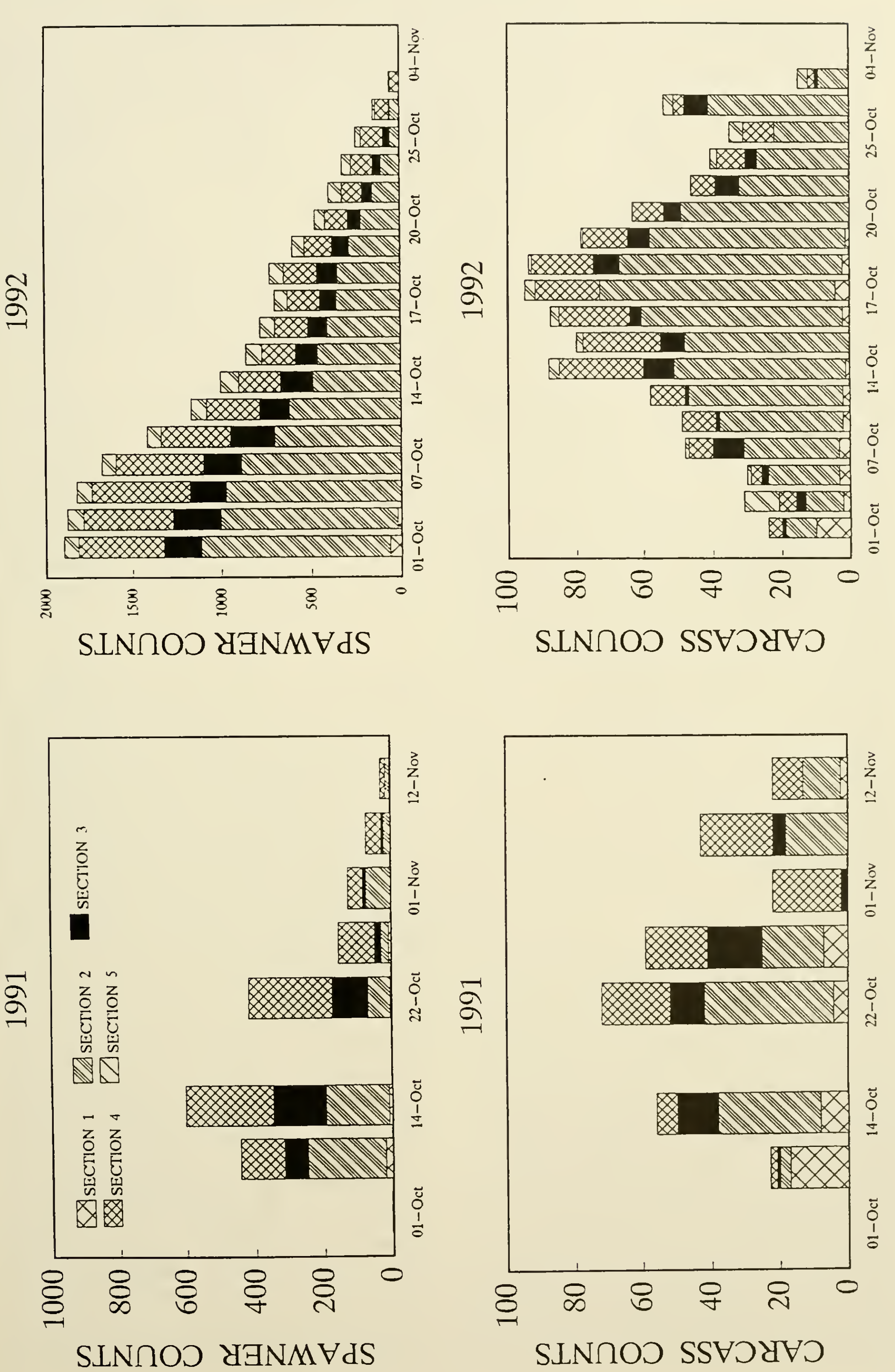

Fig. 3. Distribution of spawners (above) and carcasses (below) across sections of Taylor Creek, California, by survey date in 1991 (left) and 1992 (right).

TABLE 2. Time-density estimates of longevity from 1991 and 1992 in-stream tagging experiments (mean days spawners survived) with male and female kokanees.

	Tagged males		Tagged females	
Date	Actual tag counts	Actual and interpolated spawner days	Actual tag counts	Actual and interpolated spawner days
1991				
29 Oct	38	38.0	21	21.0
30 Oct		27.7		14.0
31 Oct		17.3		7.0
01 Nov	7	7.0	0	0.0
02 Nov		6.5		0.0
03 Nov		6.0		0.0
04 Nov		5.5		0.0
05 Nov	5	5.0	0	0.0
06 Nov		4.4		0.0
07 Nov		3.9		0.0
08 Nov		3.3		0.0
09 Nov		2.7		0.0
10 Nov		2.1		0.0
11 Nov		1.6		0.0
12 Nov	1	1.0	0	0.0
13 Nov	0	0.0	0	0.0
Total tagged spawner days		132.0		42.0
Number of tags released		38		21
Average longevity (days)		3.5		2.0
1992				
15 Oct	4	4.0	37	37.0
16 Oct	1	1.0	6	6.0
17 Oct	1	1.0	6	6.0
18 Oct	1	1.0	6	6.0
19 Oct	1	1.0	6	6.0
20 Oct	1	1.0		5.3
21 Oct	1	1.0		4.7
22 Oct	1	1.0	4	4.0
23 Oct	0	0.0	3	3.0
24 Oct		0.0		2.5
25 Oct	0	0.0	2	2.0
26 Oct		0.0		1.5
27 Oct	0	0.0	1	1.0
28 Oct		0.0		0.5
29 Oct		0.0	0	0.0
30 Oct	0	0.0	0	0.0
Total tagged spawner days		11.0		85.5
Number of tags released		4.0		37.0
Average longevity (days)		2.8		2.3

statistically significant ($P > .05$). All longevity estimates from the chamber and stream experiments were comparable to other spawning populations of kokanee and sockeye salmon in North America (Table 3), but estimates from tagged fish in the stream were consistent with the disappearance of spawners between 14 and 18 October 1991 and best represented the natural condition in Taylor Creek. For males in 1991 the regression method yielded a 20% higher population estimate than did the time-density method.

Time-density estimates of gender-specific longevities were combined with stream survey data, using equation 1, to estimate total spawning populations in Taylor Creek in 1991 and 1992: 1788 male and 1200 female spawners in 1991, and 6927 males and 7167 females in 1992. The total population estimate of 2988 spawners in 1991 was 19 times higher than the annual index survey count of 158, and the 1992 estimate of 14,094 spawners was 141 times higher than the index count of 100. The 1991 estimate of 2988 compared favorably to

TABLE 3. Mean spawning ground longevities from different North American populations of kokanees and sockeye salmon.

Population/Location	Longevity (days)	Reference
Karluk Lake	7.0	Gangmark and Fulton 1952
Brooks Lake	3.0	Eicher 1951
Wood River Lakes	1.0	Mathisen 1955
Pick Creek	3–5	Mathisen 1955
Kvichak Lake	7.6	Hartman 1959
Taylor Creek males	2.8–3.5	this study, from tagged fish in the stream
Taylor Creek females	2.0–2.3	this study, from tagged fish in the stream
Viewing chamber males	8.3	this study, tagged fish
Viewing chamber females	7.5	this study, tagged fish
Viewing chamber males	4.4	this study, untagged fish
Viewing chamber females	3.3	this study, untagged fish

our video estimate of 3520 ± 1474 prespawners aggregated near Cascade Creek in mid-September.

Spawning runs in 1991 and 1992 were the smallest on record, as were the mean body lengths of spawners (Fig. 4). Males were larger than females in both years, but the size range of males was much narrower in 1992 than in 1991 and previous years (Fig. 5).

DISCUSSION

Although 1991 and 1992 spawning populations were the smallest on record, estimates of their timing, abundance, and distribution will be very useful. An important finding was the variability and degree to which the 1 November spawning index surveys underestimated actual spawner abundance. Short spawner longevity caused much higher turnover than was previously believed and resulted in population estimates that were orders of magnitude higher than indicated by a single snapshot of the population. Since daily abundance changed over time, timing of the index survey relative to its position on the abundance curve (and the shape of the curve) is important to the consistency and accuracy of the index. The index represented 5% of the total run in 1991, but only 0.7% in 1992. In both years the 1 November index counts were made near the end of the runs (Fig. 2), and peaks for the 2 years differed by 2 weeks.

An index survey should be conducted at or near the peak of the run for several reasons. First, during peak spawning the sex ratio observed from one survey is closer to the actual sex ratio of the whole run. Second, counts near the peak capture a higher percentage of the total run. Counts during the peaks in 1991 and 1992 represented 14–20% of the total run; thus, an expansion factor of 5–7 times an index count during peak spawning could estimate total run size. In contrast, the 1 November index counts would have required expansion factors of 19–141; the magnitude and volatility of these latter factors severely compromise accuracy, precision, and thus the utility of the 1 November index. Third, variation among daily counts was lower near the spawning peak: the slope of the curve was relatively flat near the peak but became steep 1 week later. Consistency of the index, as some range of fractions of the total population, would have improved had index counts occurred near the peaks in 1991 and 1992. If three index surveys were made on 1, 8, and 15 October, the largest of these spawner counts should represent 14–20% of the total spawner abundance. If only one survey is performed, we suggest that it occur on 8 October every year.

The total spawner estimate depended on counts every 1–8 days and on estimates of longevity. The latter was more difficult to estimate with certainty. Since D_j appears in the denominator of the population estimator, the shorter the longevity, the greater the population estimate. Survival rates in the viewing chamber were higher for tagged than untagged fish, and those in the viewing chamber generally lived longer than those in the stream. Some untagged fish might have been in the stream for one or more days before transfer to the chamber, potentially causing an underestimate of longevity. Normal spawning activity and aggression were infrequent in the chamber, and these fish might have lived longer due to lower energy expenditures and stress than was experienced in the stream.

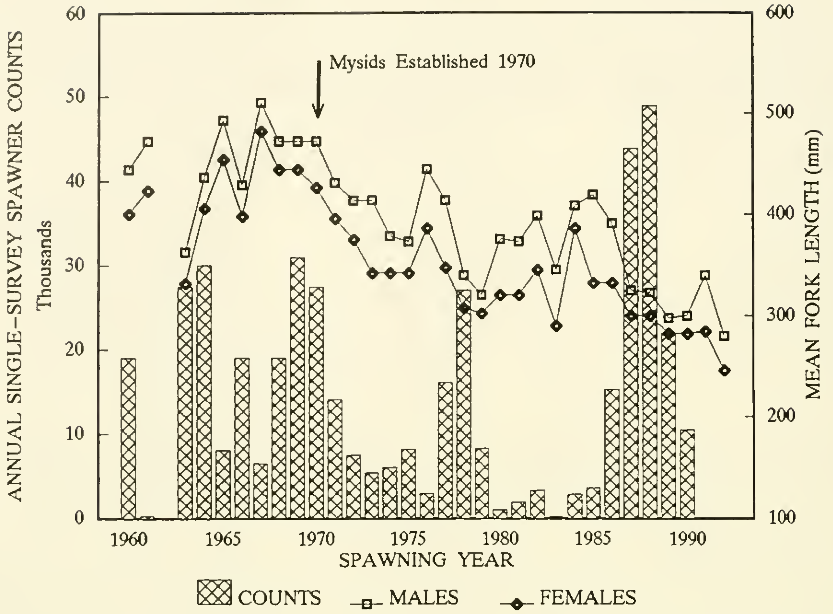

Fig. 4. Historical record of annual index survey counts of spawning kokanees in Taylor Creek, California, on or near 1 November (bars), and corresponding mean fork lengths (right vertical axis) of males (squares) and females (diamonds).

Mathisen (1955) reported that spawning females performed digging activities at least once per minute, and that males actively defended females. These activities would presumably burn the spawners' remaining energy reserves much faster than the activity observed in the viewing chamber.

Disappearance of all spawners in the stream between the peak of the 1991 run on 14 October and 18 October, 2 days after a weir blocked passage, suggested a faster turnover rate for spawners in the stream than was estimated from the viewing chamber experiment. An overestimate of longevity causes an underestimate of total abundance, and we consider the estimates derived from viewing chamber experiments to represent maxima of longevity and result in minimum estimates of spawner abundance.

The spawning population of kokanee salmon in Taylor Creek was extremely low in 1991. The annual index count on 1 November was 158 compared to counts of 3000–49,000 on similar dates during 1985–90. Index counts for the parents of the 1991 run (1987 for 4-yr-olds or 1988 for 3-yr-olds) were the largest (44,000–49,000) on record for Taylor Creek. The 1987–88 brood populations were supplemented with 590,000–850,000 fry stocked in 1984 and 1985 (Russ Wickwire, California Department of Fish and Game, Tahoe City, California, unpublished data). Reasons for the failure of these large brood years to produce large numbers of recruits are unknown and will require further study.

The magnitude of the historical index's underestimate of abundance has several important implications. Morgan et al. (1978) published a preliminary spawner-recruit relationship, based on annual index counts, and suggested that sustainable population levels dropped from 15,000 to 7000 spawners due to declines in their cladoceran prey. Although the direction and relative change in the sustainable population may be correct, actual abundance of spawners (and recruits) was severely underestimated because uncorrected index counts were used instead of estimates of absolute abundance. If a consistent relationship could be found between index counts and absolute abundance, then historical data could be adjusted and compared with contemporary data.

Taylor Creek supports most of the natural reproduction (>90%) in Lake Tahoe, but the relative contribution of other spawning areas to the lake population needs further examination. Because of severe drought conditions

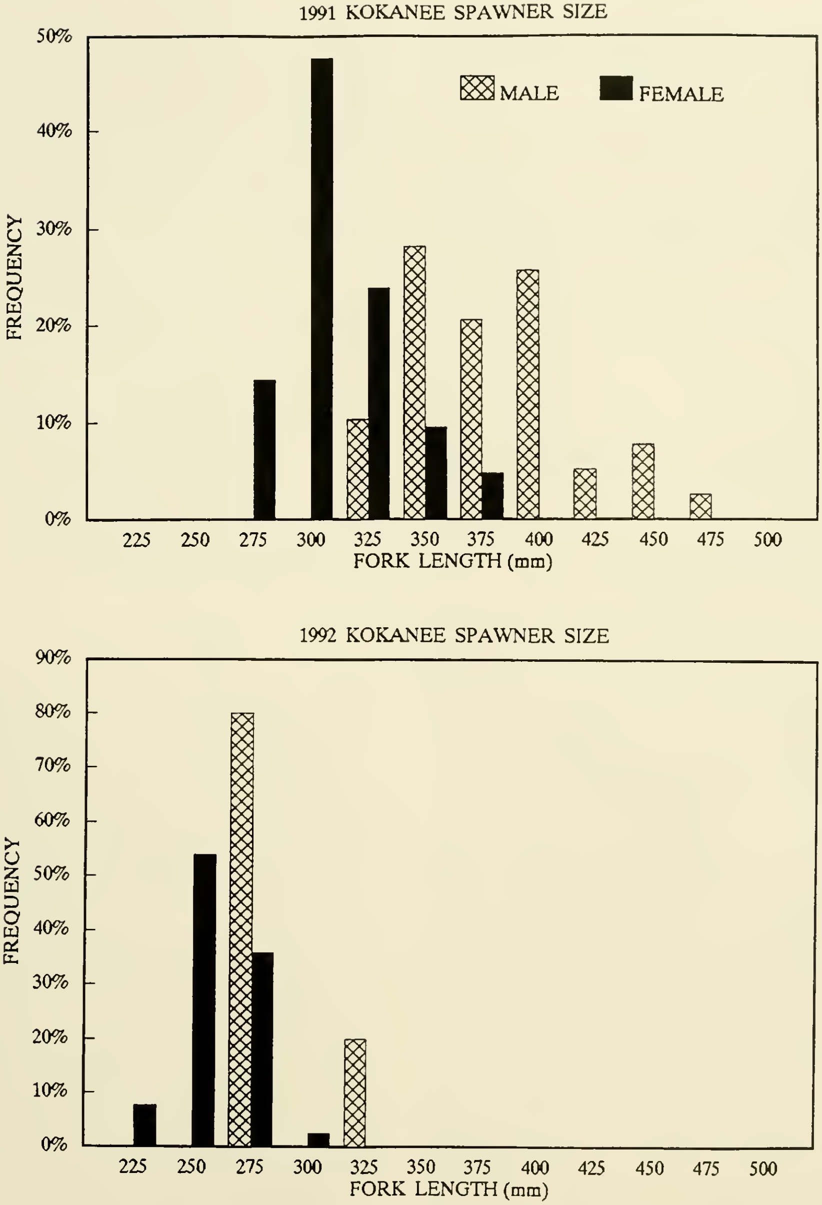

Fig. 5. Length frequency histograms for male and female spawners trapped at the mouth of Taylor Creek, California, in October 1991 (top) and 1992 (bottom).

during this study, most other streams were inaccessible to spawners due to low flow. Moreover, the 2-m drop in lake level reduced the submerged gravel habitat for shore spawners by 80% (Beauchamp et al. 1994). Absence of shore spawners could be attributed either to low overall abundance (and our inability to detect low numbers of spawners) or to low lake levels.

Spawners concentrated in the middle three sections of Taylor Creek. Given the low abundance of spawners, this distribution probably indicated preferred spawning reaches since competition for redd sites was low. Only low numbers of live males and carcasses of both sexes were found in the first reach, particularly during the first half of the run. Slower current in this section offered a "first stop" for new spawners and a place for carcasses to settle, but slow current and fine substrate provided inferior spawning habitat (Parsons and Hubert 1988).

High turnover rate of spawners and low (5–10%) percentage of carcasses observed, relative to the number expected, suggested a high demand for carcasses and perhaps for living prespawners by scavengers and predators. Cederholm et al. (1989) found that most coho salmon (*Oncorhynchus kisutch*) carcasses were retained by low-gradient streams and the adjoining forest, that few were flushed very far (<600 m) downstream, and that most (88%) carcasses removed from the stream remained within 15 m of the bank. They noted further that carcass retention was correlated positively with organic debris load and negatively with carnivore scavenging; they presented a list of 22 birds and mammals that consume carcasses. Since stream flows are regulated at relatively low discharge rates throughout the spawning season, "missing" carcasses were probably not washed out of the stream. This assumption was supported by the low number of carcasses washed against the weir or along the lake bottom in the vicinity of Taylor Creek. The concern here is that predators might remove large quantities of kokanees before they spawn and die naturally. This could be exacerbated when run sizes are low, because scavengers, prompted by the lack of carcasses, might pursue live salmon. Small spawning runs would suffer an additional burden of depensatory mortality that would accelerate the decline of the population. This disappearance of carcasses has important implications for temporal and spatial nutrient cycling of carcasses (Richey et al. 1975) and for reproductive potential of kokanees in Lake Tahoe.

The combination of record low body size and index counts for Taylor Creek spawners in 1991 and 1992 is puzzling. Abundance could be affected by parental abundance and mortality in either Taylor Creek or Lake Tahoe, but since all feeding occurs in the lake, growth can only be affected by in-lake processes. When kokanee abundance is low, density-dependent growth should produce larger spawners (Rieman and Myers 1992), but we observed the opposite. These counterintuitive results suggest that complex trophic interactions are occurring in the lake and will require careful study to identify processes that are important to kokanee productivity. Since fecundity increases with female body size (Foerster 1968), depressed growth and low population densities could severely hamper the population's ability to rebound naturally, because fewer females are each producing fewer eggs.

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FULL-GLACIAL SHORELINE VEGETATION DURING THE MAXIMUM HIGHSTAND AT OWENS LAKE, CALIFORNIA

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ABSTRACT.—Owens Valley, California, was markedly different during the Wisconsin glacial stage from what it is today. Alpine glaciers bounded the Sierra Nevada, and pluvial Owens Lake reached highstands and overflowed its natural basin. We analyzed three layers from two packrat middens, dated to ca 23,000–14,500 yr BP, obtained from Haystack Mountain (1155 m) only 10 m above and <100 m from the highstand strandline of pluvial Owens Lake. During this period vegetation near Owens Lake reflects the influence of the Tioga glacial advance and retreat on lake levels, and microclimatic effects on shoreline vegetation. Between ca 23,000 and 17,500 yr BP a Utah juniper (*Juniperus osteosperma*) and single-needle pinyon pine (*Pinus monophylla*) woodland existed at the site. In the layers dated to ca 17,500 and 16,000 yr BP, macrofossils document the presence of Rocky Mountain juniper (*Juniperus scopulorum*), a species that no longer occurs in California. It is suggested that meltwater from the retreating glacial ice inundated the Owens River Lake chain causing pluvial Owens Lake to reach its highstand. This caused an increase in effective moisture, due to high groundwater, allowing the mesophytic Rocky Mountain juniper to exist at the site.

Key words: paleoecology, packrat middens, Rocky Mountain juniper, Juniperus scopulorum, *pluvial Owens Lake, Tioga glacial stage, California.*

Few places in western North America record such a full range of Quaternary events as found in the Owens Valley of eastern California. Within the confines of the narrow Owens River corridor, never more than 33 km wide, is found evidence of late-Quaternary glacier expansions (Birkeland and Burke 1988, Bursik and Gillespie 1993), volcanic eruptions (Pakiser et al. 1964), and expansion and contraction of large "pluvial" lakes (Lajoie 1968, Smith and Street-Perrott 1983, Benson et al. 1990). Such deposits are the manifestations of great climatic and environmental changes that have occurred during the late Quaternary.

Less studied but equally striking is the record of biological changes contemporaneous and associated with pervasive changes in the physical system. Pollen from pluvial lake sediments (Leopold 1967, Batchelder 1970, Davis unpublished) has been used to reconstruct the broadscale, regional changes in vegetation. Other studies (Koehler and Anderson 1990, Jennings and Elliott-Fisk 1993, Koehler unpublished) have relied on packrat (*Neotoma*) middens, which record local vegetation changes. A combination of all proxy indicators will ultimately allow a comprehensive picture of environmental change to be revealed.

The goal of this study was to investigate the pleni- to late-glacial vegetation communities near pluvial Owens Lake (Fig. 1), which fluctuated considerably during this period. Increased effective moisture and glacial runoff during the late Wisconsin initiated a series of overflow events in the lakes that define the Owens River system (Fig. 1). The chain began in the Mono Lake Basin where Pleistocene Lake Russell (Putnam 1950) overflowed when it filled to 2175 m elevation (Lajoie 1968, Benson et al. 1990). Owens River then flowed through the Adobe Valley and mixed with waters from Long Valley en route to Owens Lake. Owens Lake periodically filled and overflowed at 1145 m. Eventually, runoff flowed to China and Searles lakes, then into Lake Manly in Death Valley (Smith and Street-Perrott 1983). Lake levels fluctuated considerably between ca 24,000 and 21,000 yr BP, followed by high and relatively stable lake levels between 21,000 and 14,000 yr BP (Smith and Street-Perrott 1983).

Six layers from two packrat middens found at 1155 m elevation in Owens Valley, Inyo County, California (Fig. 1), document full-glacial vegetation changes during the period between ca 23,000 and 14,500 yr BP. The

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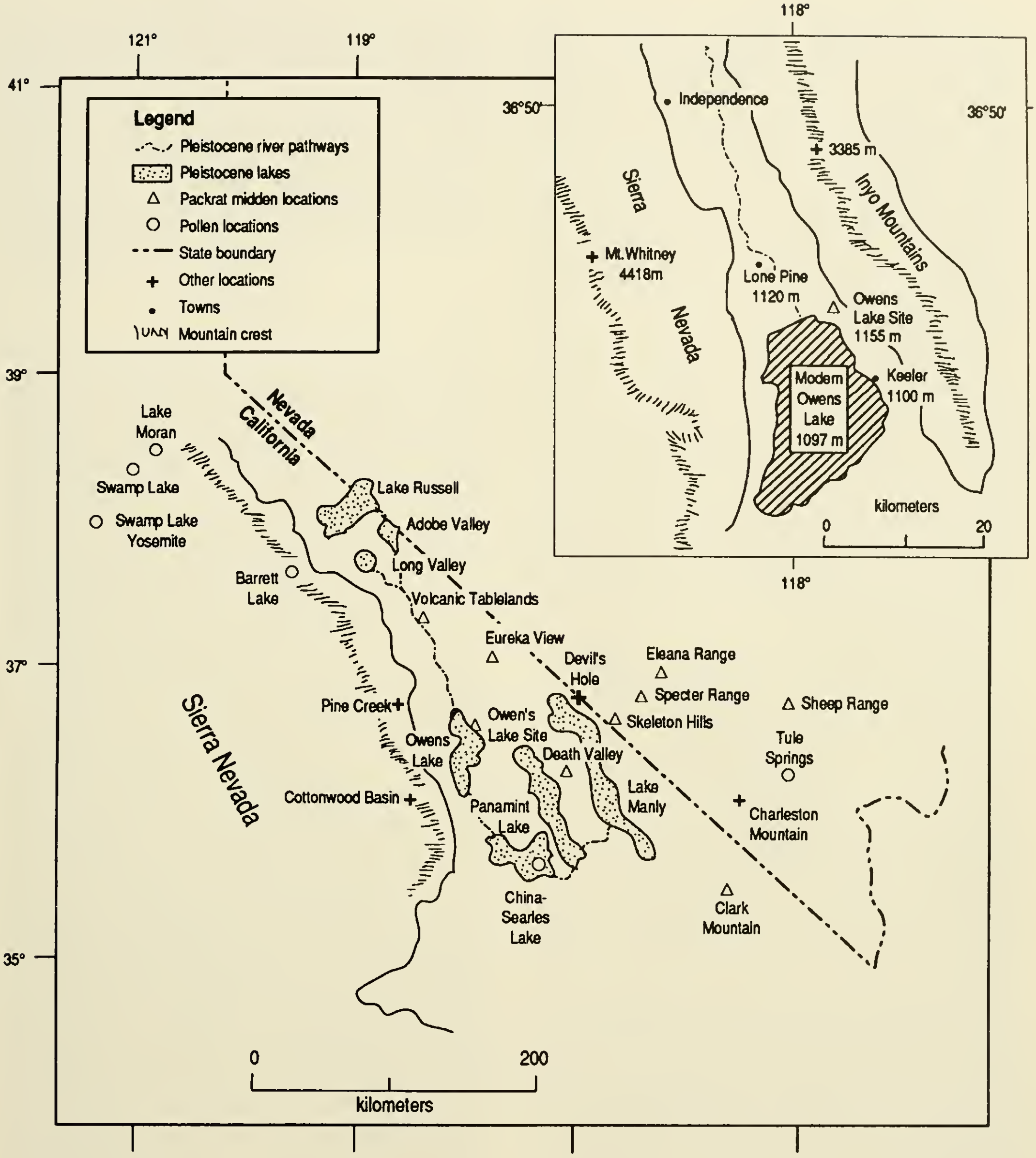
Legend
Pleistocene river pathways
Pleistocene lakes
Packrat midden locations
Pollen locations
State boundary
Other locations
Towns
Mountain crest
41°
39°
37°
35°
121°
119°
117°
115°
118°
36°50'
Lake Moran
Swamp Lake
Swamp Lake Yosemite
Barrett Lake
Nevada
California
Lake Russell
Adobe Valley
Long Valley
Volcanic Tablelands
Eureka View
Devil's Hole
Eleana Range
Specter Range
Skeleton Hills
Sheep Range
Tule Springs
Charleston Mountain
Clark Mountain
Pine Creek
Owens Lake
Owen's Lake Site
Death Valley
Lake Manly
Panamint Lake
China-Searles Lake
Cottonwood Basin
Sierra Nevada
0
200
kilometers
Independence
3385 m
Inyo Mountains
Sierra
Nevada
Mt.Whitney 4418m
Lone Pine 1120 m
Owens Lake Site 1155 m
Keeler 1100 m
Modern Owens Lake 1097 m
kilometers
0
20

Fig. 1. Map showing the Owens Lake chain and sites discussed in the text (map is after Smith and Street-Perrott 1983).

midden assemblages described here are important in deducing paleoenvironments of the region for several reasons. First, the middens occur within 10 m elevation of and <100 m away from the pluvial Owens Lake maximum highstand strandline. Second, the occurrence within several middens of plant macrofossils of Rocky Mountain juniper (*Juniperus scopulorum*), a tree not found today in California, suggests that pluvial highstands during glacial retreats produced a unique microclimate at this nearshore location.

THE SITE

Owens Valley lies between the massive Sierra Nevada to the west and the Inyo-White Mountain ranges to the east. The Sierra Nevada rise from California's Great Valley, with a gentle westward gradient of 6% toward a lofty crest that contains some 500 summits over 3660 m, with 11 peaks over 4260 m. The eastern escarpment of the Sierra plummets, with a ca 14% gradient, as much as 3050 m into the Owens Valley. The graben forming Owens Valley ranges ca 13–33 km wide, with an average elevation of only 1160 m. The eastern flank of the Owens Valley is bounded by the Inyo-White Mountain chain, with a crest elevation that averages ca 2900 m.

Two indurated packrat middens, containing six stratigraphic units, were found at a single location on Haystack Mountain, ca 3 km east of the Inyo Mountains (36°36′N, 118°05′W; Fig. 1). The outcrop where the middens were found is of a spheroidally weathered Cretaceous granite (Ross 1967) and faces southeast. At 1155 m the site is located ca 100 m north and 10 m above the Owens Lake highstand strandline (1145 m).

Currently the local vegetation is dominated by a saltbush (*Atriplex* spp.)/hopsage (*Grayia spinosa*)/sagebrush (*Artemisia* spp.) community on the valley floor, while wolfberry (*Lycium andersonii*), mallow (*Sphaeralcea* spp.), and various species of the grass family occupy the immediate rock outcrop. Creosote bush (*Larrea tridentata*) and bursage (*Ambrosia dumosa*) are found locally on well-drained sites, and greasewood (*Sarcobatus vermiculatus*) occurs on sites with alkaline soils and high water tables.

Vegetation that occurs from 1150 m on the alluvial fans to 1950 m is represented by a Mojave Desert community dominated by creosote bush and bursage. Joshua tree (*Yucca brevifolia*), single-needle pinyon pine (*Pinus monophylla*), and spiny menodora (*Menodora spinescens*) occur in a transition zone (1950–2100 m) that trends into a pinyon–Utah juniper (*Juniperus osteosperma*) woodland at ca 2100–2900 m. In the southern Inyo Mountains subalpine trees are found only on peaks above ca 2900 m. Limber pine (*Pinus flexilis*) is common in this region, with lesser amounts of bristlecone pine (*Pinus longaeva*), fernbush (*Chamaebatiaria millefollium*), and sagebrush. Several individuals of Sierra juniper (*Juniperus occidentalis* var. *australis*) also grow in the Inyo Mountains (Vasek 1966).

The nearest weather stations, Lone Pine (1120 m, 8 km west of the site) and Keeler (1100 m, 16 km southeast of the site), record an annual precipitation of 127 mm/yr and 80 mm/yr (Lee 1912, Elford 1970), respectively. Precipitation occurs primarily in the winter months with some rainfall in the summer months as isolated thunderstorms. Precipitation of 203–304 mm/yr has been estimated for the pinyon woodlands of the White Mountains at elevations of 1525–2135 m (St. Andre 1965).

METHODS

Three layers (A–C) were found in each of the two middens (HM1 and HM2) and were separated along stratigraphic planes. Once separated, the samples were disaggregated in distilled water in a covered bucket. This was done to prevent contamination by modern pollen. The disaggregated middens were sieved through a number 20-mesh (0.85-mm) screen with the decant saved for pollen analysis.

The midden debris was air-dried and hand-sorted under a dissecting microscope (7–40X magnification). Plant macrofossils were identified from reference materials. Interpretation of the macroremains is based on a relative abundance scale with 5 = >200 macroremains, 4 = 100–200, 3 = 30–99, 2 = 2–29, and a single specimen = 1 (Van Devender et al. 1987). Radiocarbon data were obtained primarily on fecal pellets (Table 1).

Processing for fossil pollen followed Faegri and Iverson (1989) and included the addition of *Lycopodium* tracer tables (Stockmarr 1971), acetolysis, staining, and suspension in silicon oil. A 300-grain count (range = 262–361; Table 3) of terrestrial pollen types was made at 400X magnification. The count excluded tracer, deteriorated, and aquatic pollen types. Pollen percentages were calculated based on the total terrestrial pollen counted in each sample. Many of the pollen types were identified to

TABLE 1. Radiocarbon analysis of the Owens Lake site (1155 m), Inyo County, California.

Sample	Radiocarbon years B.P.	Dated material	Lab number
HM2A	14,870 ± 130	Dung	Beta-39274
HM2C	16,010 ± 330	Dung	Beta-36732
HM2B	17,680 ± 150	Dung	Beta-35503
HM1A	20,590 ± 210	Debris	Beta-40000
HM1B	20,960 ± 240	Dung	Beta-34833
HM1C	22,900 ± 270	Dung	Beta-39273

family; however, some types were broken into morphological categories. *Pinus* pollen was separated into the haploxylon (white pine) and diploxylon (yellow pine) groups. *Ephedra* pollen was divided into *E. viridis* and *E. californica* pollen types. *Purshia-Cercocarpus* pollen types were discriminated from Rosaceae, and *Sarcobatus* was separated from other members of the Chenopodiaceae-*Amaranthus* (Cheno-am) group.

RESULTS

Macrofossils recovered from the middens document plants typically found in the pinyon-juniper zone of the Inyo Mountains. The exception to this is the occurrence of Rocky Mountain juniper (*Juniperus scopulorum*), which does not occur today in California. Fossil pollen recovered from the middens represents plants found within the midden as well as local species that either are avoided by packrats or occur beyond their foraging range (Anderson and Van Devender 1991).

Midden macrofossils are represented by the presence of Utah juniper in all samples (Table 2). Green ephedra (*Ephedra viridis*), wild rose (*Rosa woodsii*), *Menodora*, and pinyon pine occur in most of the other samples. Nevada greasebush (*Forsellesia nevadensis*) and Joshua tree also occur in several of the older middens (ca 22,900–20,590 yr BP). Rocky Mountain juniper is present in two middens dated to ca 17,680 and 16,010 yr BP.

Pollen identified from the middens generally supports macrofossil evidence (Table 3). Exceptions to this are the high amounts of *Artemisia* (ca 6–50%) and moderate amounts of Cheno-ams (ca 5.5–18%). High variability within pollen percentages may be due to the uncertain association with deposition time (months to centuries) and the year-to-year variability in pollen production.

DISCUSSION

During the Pleistocene several alpine glacier advances sculpted the Sierra Nevada, with at least three stages recorded during the late Wisconsin (Bursik and Gillespie 1993). The most recent episode, the Tioga advance, occurred during the full-glacial period, ca 21,000–18,000 yr BP. Significant advances in glacial chronology have been made in the last decade. Experimental analysis of the accumulation of cosmogenic Cl-36 suggests that maximum Tioga glaciation occurred prior to ca 21,000 yr BP (Phillips et al. 1990). Radiocarbon dates of 21,000 ± 130 yr BP (Lebetkin 1980) from tufa underlying an alluvial fan of inferred Tioga-age at Owens Lake (Fullerton 1986) and of 19,050 ± 210 yr BP on basal rock varnish from an outermost Tioga moraine in Pine Creek (Dorn et al. 1987) also support a maximum advance before this time. Timing on Sierra Nevada deglaciation is recorded by dates of glaciolacustrine sediments from mid-elevation west-side lakes (Swamp Lake ca 15,565 yr BP [1957 m; Batchelder 1980], Lake Moran ca 14,750 yr BP [2018 m; Edlund and Byrne 1991], Swamp Lake Yosemite ca 13,350 yr BP [1554 m; Smith and Anderson 1992]) and rock varnish dates on recessional Tioga moraines of ca 13,910 yr BP from Pine Creek (1830 m; Dorn et al. 1987). Dates from near the Sierran crest at Barrett Lake (2816 m) of ca 12,500 yr BP (Anderson 1990) and ca 10,300 yr BP in the Cottonwood Basin (ca 3000 m elevation; Mezger 1986) document high-elevation deglaciation on the east side.

The presence of ice in the Sierra Nevada had a significant impact on paleoenvironments within Owens Valley. The Owens River watershed covers ca 8500 km^2, with nearly all of its runoff originating in the 16% of this area lying in the eastern Sierra Nevada (Lee 1912, Smith and Street-Perrott 1983). Thus, as melting glaciers retreated, lakes within the valley would periodically fill, overflowing to a downstream lake in the chain. Based on glacial features, the glacial ice west of the Sierra Nevada crest increased the average elevation by ca 50 m in the south (Gillespie 1982, Mezger 1986) to as much as 300 m in the Yosemite National Park area (Alpha et al. 1987). Elevational increases east of the crest were insignificant because their glaciers were largely restricted to steep valleys. During the period of maximum ice extent within the Sierra Nevada, the increased average elevation of the range, caused by the combination of upwards of ca 600 m of ice plus the ca 100 m lowering of sea levels, may have had two effects on the Owens Valley and Inyo-White Mountains to the east. First, the higher average elevation of the Sierra Nevada intensified the rainshadow effect, as witnessed by the limited glaciation within the Inyo-White Mountains (Elliott-Fisk 1985, Swanson et al. 1993). Second, accumulation of

TABLE 2. Plant macrofossils identified from the Owens Lake site (1155 m), Inyo County, California. Relative abundance is based on >200 specimens = 5, 100–200 = 4, 30–99 = 3, 2–29 = 2, and a single specimen = 1.

Sample unit Sample age yr B.P.	HM2A 14,870	HM2C 16,010	HM2B 17,680	HM1A 20,590	HM1B 20,960	HM1C 22,900
TREES/SHRUBS						
Juniperus osteosperma	4	4	4	3	5	5
Juniperus scopulorum	—	3	2	—	—	—
Pinus monophylla	—	—	2	2	3	2
Ephedra viridis	2	—	2	5	5	5
Menodora spinescens	2	2	—	—	2	2
Mirabilis bigelovii	—	—	—	2	2	3
Eriogonum cf. *fasciculatum*	—	—	2	—	—	—
Forsellesia nevadensis	—	—	—	3	2	5
Artemisia tridentata	—	—	—	—	—	1
Chrysothamnus teretifolius	2	2	—	2	2	2
Ericameria cuneata	2	2	2	2	2	2
Tetradymia sp.	—	2	—	—	—	—
Atriplex polycarpa	—	—	—	—	1	—
Atriplex confertifolia	1	—	—	—	—	—
Grayia spinosa	—	1	—	—	—	—
Rosa woodii	2	2	2	—	—	2
Coleogyne ramosissima	—	—	—	—	1	—
Yucca cf. *brevifolia*	—	—	—	—	2	—
HERBS						
Sphaeralcea ambigua	2	—	—	—	2	2
Cirsium sp.	—	—	2	1	2	—
Boraginaceae	—	—	—	2	—	—
Amsinkia sp.	—	—	—	—	2	—
Cryptantha sp.	—	—	—	—	2	—
Plagybothrys spp.	—	—	—	—	—	2
Salvia sp.	—	—	—	—	1	—
Orthocarpus sp.	—	2	—	—	—	—
SUCCULENT						
Opuntia basilaris	1	—	2	2	4	4
GRASS						
Oryzopsis hymenoides	—	—	—	2	2	2

ice in the central Sierra Nevada probably deflected storm tracks further south than today and at a more frequent rate, as witnessed by wetter conditions in the modern Mojave Desert at that time (Spaulding and Graumlich 1986).

While the lake-level fluctuations at Owens Lake are poorly known, the periods of highstands and overflow can be estimated from the detailed records of pluvial Lake Russell and Searles Lake (Smith and Street-Perrott 1983, Benson et al. 1990). Owens Lake either received overflow from (Lake Russell) or contributed to (Searles Lake) pluvial lakes. Lake levels at Searles were generally high to overflowing between ca 25,000 and 10,000 yr BP. Between ca 21,000 and 15,000 yr BP a continuous highstand is inferred. Lake levels then returned to moderately low levels after ca 15,000 yr BP (Smith and Street-Perrott 1983) or ca 14,000 yr BP (Benson et al. 1990). For Lake Russell, lake-level chronologies suggest intermediate levels from at least 35,000 yr BP until a highstand after 15,000 (ca 14,000 or 13,000 yr BP; Benson et al. 1990).

During the full-glacial, the Owens Lake midden site was located in a transitional position between the full-glacial single-needle pinyon-juniper woodlands of the Mojave Desert and the Utah juniper–limber pine woodland of the southern Great Basin. In the rain shadow of the Sierra Nevada, the Eleana Range (1810 m) records limber pine and steppe shrubs (Spaulding 1990). North of the Owens Lake site at slightly higher elevations, colder conditions are recorded by the occurrence of Utah juniper and sparse limber pine at Eureka View (1430 m) at ca 14,700 yr BP (Spaulding 1990) and Utah juniper and Great Basin desert shrubs at the Volcanic Tablelands (Jennings and Elliott-Fisk 1993). Pinyon pine was not found in Death Valley where Utah juniper existed with a yucca semidesert (260–1280 m; Wells and Woodcock 1985). South of

TABLE 3. Percentages of identified pollen types from the Owens Lakes site (1155 m), Inyo County, California.

Sample unit Sample age yr B.P.	HM2A 14,870	HM2C 16,010	HM2B 17,680	HM1A 20,590	HM1B 20,960	HM1C 22,900
Tracer	27.0	20.0	16.0	42.0	85.0	76.0
Deteriorated	5.0	30.0	10.0	15.0	13.0	3.0
Abies	0.0	0.3	0.0	0.0	0.3	0.0
Pinus haploxylon	9.4	9.7	3.0	9.2	30.4	9.0
Pinus diploxylon	12.2	1.7	1.5	1.5	0.9	9.0
Cupressaceae	13.6	23.4	32.5	22.5	36.6	34.7
Ephedra viridis-type	0.6	2.5	0.6	0.4	1.2	1.0
Ephedra californica-type	0.8	1.4	0.0	0.0	0.0	0.3
Menodora	0.0	0.3	0.0	0.0	0.3	0.0
Symphoricarpos	0.0	0.0	0.0	0.0	0.3	0.0
Quercus	0.0	0.0	0.0	0.0	0.3	0.0
Ambrosia	0.6	1.1	0.0	3.4	1.6	0.3
Artemisia	50.1	39.6	43.8	45.0	5.9	17.0
Cirsium	0.3	0.0	0.0	0.0	0.0	0.0
Other Compositae	1.1	1.7	1.8	5.3	7.1	6.4
Cheno-ams	5.5	10.6	6.4	7.6	9.6	18.0
Sarcobatus	4.7	5.6	8.8	4.6	2.8	4.2
Rosaceae	0.0	0.0	0.0	0.0	0.3	0.0
Purshia	0.0	0.0	0.0	0.0	0.9	0.0
Ceanothus	0.0	0.0	0.0	0.0	0.3	0.0
Eriogonum	0.3	0.6	0.3	0.0	0.0	0.0
Solanaceae	0.0	0.0	0.9	0.0	0.0	0.0
Cruciferae	0.0	1.1	0.0	0.0	0.3	0.0
Leguminosae	0.6	0.0	0.0	0.4	0.6	0.0
Polemonaceae	0.0	0.0	0.3	0.0	0.0	0.0
Gramineae	0.3	0.6	0.0	0.0	0.0	0.0
Terrestrial total	361	359	329	262	322	311
AQUATICS						
Typha	0.0	0.0	0.0	0.0	1.0	0.0

the Owens Lake site, the Mojave Desert full-glacial vegetation records the widespread occurrence of a pinyon-juniper woodland (Spaulding 1990).

Records from the Owens Lake site (1155 m) and Skeleton Hills (925 m; Spaulding 1990) are the only documentation of pinyon pine during the full-glacial at this latitude. The lower limit of pinyon pine is recorded in the Skeleton Hills at 925 m. In Owens Valley the upper limit of pinyon is constrained between 1155 m (this report) and 50 km north in the Volcanic Tablelands at 1340 m (Jennings and Elliott-Fisk 1993). Despite the absence of pinyon at Death Valley, these sites define the northern distribution of pinyon in the Mojave Desert during the full-glacial.

The most interesting macrofossil found in the midden series dating 17,680 and 16,010 yr BP is Rocky Mountain juniper. This tree is not found in California today but occurs in the Charleston Mountain area of southwestern Nevada, ca 225 km east of the site. The elevational and latitudinal migration of Rocky Mountain juniper is well understood in the southeastern and central Great Basin (Thompson 1990). Using terpene variations, Adams (1983) provided evidence for Rocky Mountain juniper colonization in post-glacial environments within the extreme northern and southern extensions of its range, suggesting migration routes along pluvial lake corridors. Rocky Mountain juniper is generally restricted to regions that lack pronounced summer droughts (West et al. 1978, Thompson 1988). In the southern part of its range, Rocky Mountain juniper is restricted to riparian settings or areas of shallow groundwater and springs (Adams 1983). This information is germane to the history of lake-level fluctuations within the Owens Valley area.

The occurrence of Rocky Mountain juniper at the Owens Lake site is thus partially explained by local climatic factors associated with pluvial lake highstands. Its existence around Owens Lake between ca 17,680 and 16,010 yr BP was probably influenced by relatively high water tables or locally humid conditions associated with the highstand at that time. Its subsequent absence by 14,870 yr BP was probably a result of declining lake levels.

CONCLUSIONS

The Owens Lake midden site provides evidence for paleoenvironmental change along the shore of Owens Lake spanning the full-glacial Tioga advance. The midden sequence from ca 23,000 to 17,680 yr BP records a juniper-pinyon woodland with associated xeric upland desert scrub and possible Joshua tree. The presence of Rocky Mountain juniper at 17,680 and 16,010 yr BP suggests a mesophytic association due to the presence of Owens Lake. In apparent contradiction, drier conditions are recorded after ca 17,500 yr BP at nearby locations (Death Valley, Wells and Woodcock 1985; Skeleton Hills, Spaulding 1990; Sheep Range, Spaulding 1981), and this is supported at the Owens Lake site as pinyon pine is not recorded after 17,680 yr BP.

Dated moraines record the timing of the Tioga glaciation (Dorn et al. 1987, Bursik and Gillespie 1993). Prior to ca 19,000 yr BP, pluvial lake highstands are not recorded (Bursik and Gillespie 1993), as some available moisture was sequestered to the Owens Lake chain in the alpine ice of the Sierra Nevada. A deglaciation with possible readvances, between ca 19,000 and 13,000 yr BP, caused the lakes of the Owens River to achieve highstands. The close proximity of the Owens Lake highstand allowed sufficient effective moisture for Rocky Mountain juniper to exist close to the midden site (within 10 m elevation and <100 m distance from the lake).

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REDBAND TROUT RESPONSE TO HYPOXIA IN A NATURAL ENVIRONMENT

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ABSTRACT.—Redband trout (*Oncorhynchus mykiss gairdneri*) were observed approximately every 2 weeks in an intermittent southwest Idaho stream between August and December 1991. Instantaneous daytime dissolved oxygen concentration and water temperature declined from 4.0 to <2 mg/L and 17 to 2°C, respectively, during this period. Redband trout declined from a maximum captured of 48 on 28 August to 1 on 8 November in one series of pools. As conditions approached hypoxia, trout exhibited little movement and positioned themselves in water just deep enough to cover their dorsal fin. High densities of speckled dace (*Rhinichthys osculus*) were also present in each pool until drying. The response of these fish to such extreme habitat conditions is probably a primary factor accounting for their distribution within arid landscapes.

Key words: Oncorhynchus mykiss gairdneri, *redband trout,* Rhinichthys osculus, *oxygen tolerance, aquatic surface respiration, intermittent streams, desert fishes.*

Headwater streams often become intermittent during summer (Williams 1987). Fish unable to migrate to perennial reaches are trapped in isolated pools where they may be subjected to lethal conditions. Observations of behavioral responses and survival of stream fishes in these conditions are few (Tramer 1977, Matthews et al. 1982, Mundahl 1990). Conditions associated with isolated pools in intermittent streams include lack of space and cover (Capone and Kushlan 1991), widely fluctuating and often lethal pH (Capone and Kushlan 1991), temperature (Huntsman 1942, 1946, Bailey 1955, John 1964, Matthews et al. 1982, Mundahl 1990), and dissolved oxygen (Tramer 1977). The ability of fish to survive harsh habitat conditions (*sensu* Matthews 1987) has been attributed to physiological (Matthews 1987) and behavioral adaptations (Kramer 1987).

Arid-land rainbow trout (*Oncorhynchus mykiss*) occur in southern Oregon, southwestern Idaho, and northern Nevada. Behnke (1992) believes these fish are a form of Columbia River redband trout (*O. m. gairdneri*) that have adapted to arid-land streams characterized by extremes in stream flow, temperature, and dissolved oxygen; little is known of their life history or ecology (Kunkel 1976, Behnke 1992). This paper describes the demise of most and the survival of a few redband trout under low dissolved oxygen concentrations in an intermittent stream in southwest Idaho.

STUDY AREA

The study was conducted on Sinker Creek, a second-order tributary of the Snake River in southwestern Idaho, approximately 1 km from the confluence with the East Fork of Sinker Creek (T4S, R2W, Sec. 19, 20, Owhyee County, Idaho). Elevation of the study area is 1100 m. The geomorphology of the area is characterized by coarse alluvial fill interspersed with bedrock in a basalt canyon. Riparian areas are mostly unvegetated, except immediately adjacent to pools where willow (*Salix* sp.) clumps overhang the stream channel. Dewatered streambed areas are unvegetated. The watershed is subjected to summer livestock grazing.

During 1991, streams throughout southwestern Idaho were flowing at far below normal levels (U.S. Geological Survey 1992). Sinker Creek upstream of the confluence with the East Fork of Sinker Creek was dry with the exception of a few isolated reaches. Data are presented from the largest wetted reach that consisted of five pools (A–E, sequentially, downstream) separated by shallow riffle areas along a 300-m reach.

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METHODS

Fish populations and habitat conditions were monitored approximately every 2 weeks between 14 August and 5 December 1991. Fish behavior was observed for 30–60 min prior to sampling. High-water clarity and limited pool area and depth facilitated direct observations, especially later in the study. Beginning 28 August, a Smith-Root battery-powered backpack electrofisher (Model 11A) was used to collect all redband trout in each pool. Total length and weight were recorded (weights were not taken prior to 24 October), and trout >100 mm were differentially fin clipped to identify fish from individual pools (there was a distinct size class break at 100 mm; trout <100 mm are herein referred to as small and trout >100 mm as large).

During each visit water temperature and dissolved oxygen (DO, mg O_2/L) were measured with a YSI (Yellow Springs Instrument Company, Inc.) Model 57. Measurements were made between 1000 and 1430 h on all dates at several locations throughout each pool at surface, mid-depth, and bottom.

Pool surface area was determined as a rectangle by averaging several length and width measurements; depth was measured at the same locations as temperature and DO. Measurements continued until a pool dried or until 5 December when continuous flow returned to the stream. On 14 August 1991 pieces of plastic flagging were placed in the dry streambed between pools and weighted down with leaves so flow events between sampling dates could be detected; none were detected prior to 5 December.

RESULTS

On 14 August 1991 one redband trout was observed in pool B and three in pool D; numerous speckled dace (*Rhinichthys osculus*) were observed in all pools. Water temperature and DO ranged from 7°C and 1.5 mg/L, where water emerged from the substrate, to 28.5°C and 11.5 mg/L at the end of the wetted reach downstream of pool E.

On 28 August 48 redband trout were captured: 1 in pool A, 23 in pool B, 9 in pool C, 15 in pool D, and 0 in pool E. Pool areas ranged from 8 to 27 m^2. Water temperature and DO ranged from 16.8 to 18.5°C, and 1.7 to 4.6 mg/L, respectively, at the up- and downstream ends of the wetted reach. Between 28 August and 11 October all pools and riffles went dry with the exception of pool D. No trout were found in any pool other than pool D after 28 August. Numerous (>100) speckled dace (mean length 25 mm) were present in each pool until drying.

Between 28 August and 5 December the volume and surface area of pool D decreased from 10.5 to 0.5 m^3 and 27 to 4 m^2, respectively. Maximum pool depth decreased from 81 to 18 cm, and mean pool depth went from 56 to 13 cm. Dissolved oxygen decreased from 3.7 mg/L on 28 August to 1.6 mg/L on 1, 6, and 11 October. Between 24 October and 22 November, DO increased slightly to 2.0–3.0 mg/L. Water temperature dropped throughout the study period (Fig. 1) and was less than 10°C after 6 October. On all dates DO was slightly higher at the surface than at the bottom (mean difference = 0.2 mg/L). On 22 November a thin layer of ice covered half of pool D. On 5 December, when continuous flow returned to Sinker Creek, water temperature was 5°C and DO was 9.5 mg/L (Fig. 1).

Redband trout in pool D declined from a maximum of 33 captured on 20 September to 1 on 16 November (Fig. 1). The increase in trout captured between 28 August and 20 September was probably due to increased capture efficiency caused by a reduction in pool area and not from relocation of trout from other pools. No marked trout were captured in a pool different from the one in which they were originally captured. Recapture success was ca 50% in September and October and 100% in November. In November there was little space left in pool D for redband trout to hide, and the pool was more accessible to electrofishing.

On several occasions dead redband trout were found along the edge of pool D: one on 1 October, two on 11 October, and five on 8 November. No dead redband trout were recovered from any other pools. Dead redband trout had not been scavenged, and no sign of scavengers was apparent during any site visit. Of the missing redband trout, most were not accounted for, and those that were found were all >140 mm. Smaller trout may have been buried in the extensive decaying leaf material present in each pool. On 1 October two trout died and on 11 October one trout died as a result of electrofishing.

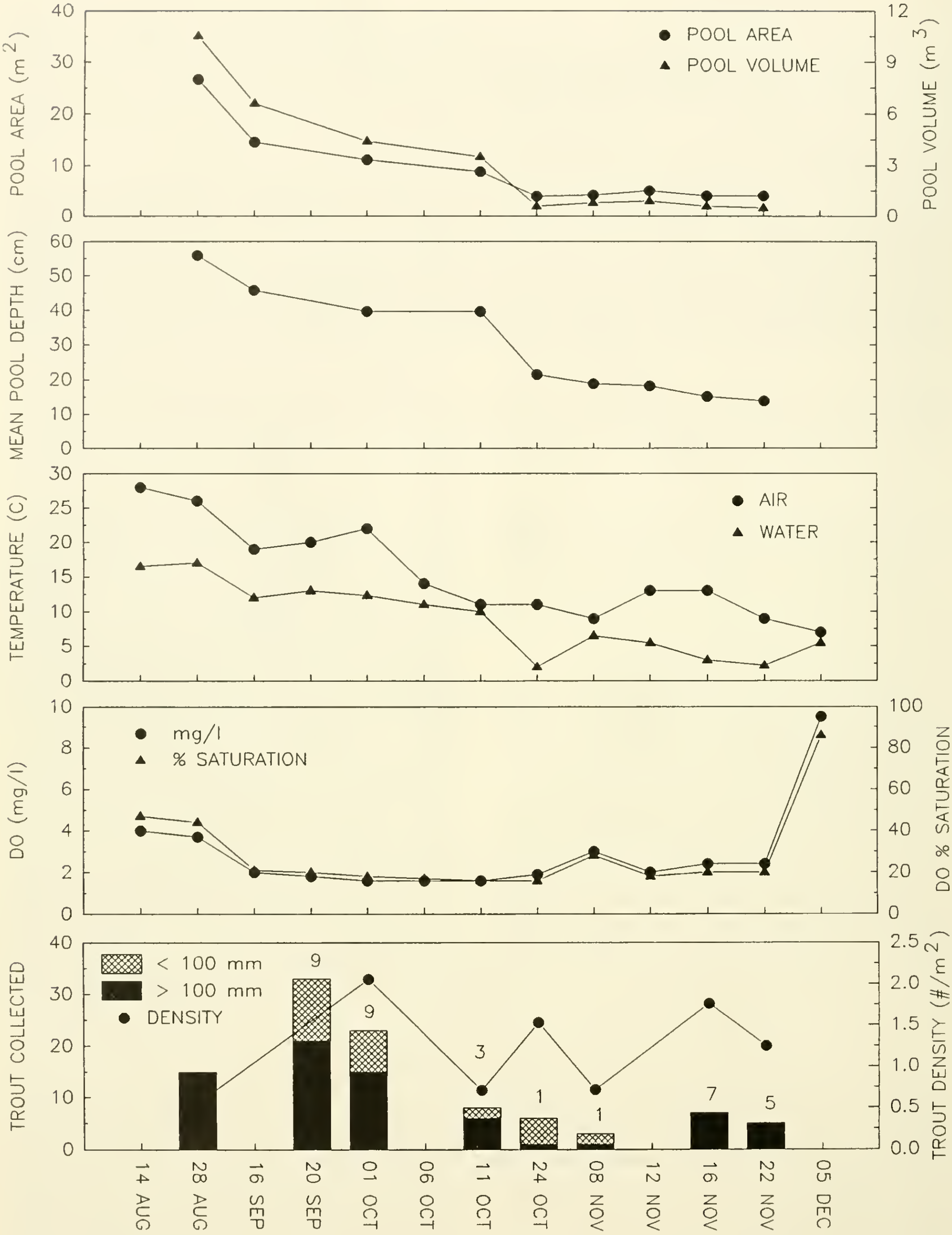

Fig. 1. Sinker Creek pool D volume, area, mean depth, air and water temperature, dissolved oxygen concentration and percent saturation, and trout numbers and densities (#/m^2) between 14 August and 5 December 1991. Trout numbers and densities on 8, 16, and 22 November include trout transferred from the East Fork of Sinker Creek. ■ are trout >100 mm (large). ▩ are trout <100 mm (small). There was a distinct size class break at 100 mm. Numbers above bars are recaptures of previously marked trout (>100 mm). Pool dimensions were not measured on 20 September, 6 October, and 5 December. Trout were not collected on 14 August, 16 September, 6 October, 12 November, and 5 December.

Prior to 24 October redband trout were observed swimming and surfacing throughout the pool. Approximately 60% of the pool could be effectively observed up to this date. Between 11 October and 24 October pool D shrank by 83% (Fig. 1), and the entire pool could now be observed. From this date on, redband trout were generally biding beneath small boulders in the middle of the pool or among the leaf debris along the shallow pool margins. Trout were rarely seen swimming around the pool. After being captured and returned to the pool, trout typically moved to shallow water along the shoreline and faced outward. While positioned along the pool edge, they occupied water just deep enough to cover their backs and "gulped" at the air-water interface. They remained in this position for at least 1 h. This post-capture behavior was probably a response to the stress of electrofishing. Speckled dace, whose densities were high throughout the study, showed no obvious change in behavior during the four months of observation.

On 8 November six large redband trout (145–222 mm) were captured by electrofishing and transferred from the perennial East Fork of Sinker Creek to pool D. Water temperature in the East Fork was 8.5°C and DO was 9.8 mg/L. In pool D water temperature was 6.5°C and DO was 3.0 mg/L. This transfer took ca 15 min. Immediately upon being placed in pool D, the redband trout moved to shallow margins of the pool and began "gulping" at the air-water interface. Over the next hour they remained along the edge of the pool facing outward with their dorsal fin just breaking the water surface. Opercular movements remained rapid during this time. The one original pool D large redband trout remained under a boulder in the middle of the pool and did not interact with the transplanted redband trout; the two remaining small trout were not observed.

On 12 November water temperature was 5.5°C and DO was 2.0 in pool D. Because the electrofishing unit was not functional, no redband trout were captured, but several were observed along the pool margins facing outward. On 16 November seven large redband trout were collected (one original pool D trout and the six East Fork redband trout). The two remaining small redband trout could not be found. The six transplanted East Fork redband trout had all lost weight (1–8 g) since being transferred 8 days earlier; the accuracy of the scale was ca ±1 g. On 22 November three of the transplanted redband trout maintained the same weight as on 16 November, one lost 1 g, and two could not be found. The weight of the original pool D redband trout declined from 66 g on 11 and 24 October to 63 g on 8 November, 62 g on 16 November, and 60 g on 22 November.

DISCUSSION

One of 48 redband trout survived at least 114 days in DO <4 mg/L, and 4 redband trout transplanted from the perennial, high DO (9.8 mg/L) East Fork of Sinker Creek survived 43 days at DO <2.5 mg/L. Water temperature declined from 17 to 2°C during this period. Additional survival would probably have occurred if not for repeated electrofishing. The ability of arid-land redband trout to withstand harsh habitat conditions has been suggested by Wishard et al. (1984) and Behnke (1992). Behnke (1992) reported fishing for and catching arid-land redband trout in intermittent stagnant pools in Oregon. There are a few studies on water temperature tolerance of native western trout species (e.g., Lee and Rinne 1980), but no field observations have been previously made of native trout responses to low DO.

Effects of low DO on rainbow trout were summarized by Davis (1975). Negative effects of low DO first become apparent at 5–6 mg/L (Davis 1975). Responses of adult rainbow trout to DO <5 mg/L or <50% saturation include elevated breathing amplitude and buccal pressure (Hughes and Saunders 1970), reduced heart rate (Randall and Smith 1967), reduction in swimming speeds (Kutty 1968), and reduced capacity for anaerobic metabolism (Kutty 1968).

A possible explanation for the survival of redband trout in this study might be that a seep with higher DO was entering this pool. We looked for such a source by measuring temperature and DO throughout the pool on each sampling date and by digging shallow groundwater wells into the streambed on 8 November. There was little variation in temperature and DO within pools for any date. Groundwater temperature was 2.5°C and DO was 1 mg/L. Groundwater typically contains little or no dissolved oxygen (Hem 1985).

Probable factors contributing to fish survival included a long acclimation period (Shepard 1955, Davis 1975), especially when compared to laboratory studies, sedentary behavior (Davis 1975), declining air and water temperatures as the study progressed (Fig. 1), and lack of water velocity in either pool so that energy expenditures would have been minimal (Davis 1975). Sinker Creek probably became intermittent in May or June, after snowmelt runoff. Fish unable to escape downstream to the perennial East Fork of Sinker Creek had many weeks to become acclimated to the gradually deteriorating conditions.

Increased acclimation improves trout survival in low DO. Shepard (1955) showed that with sufficient acclimation time lethal DO levels for brook trout (*Salvelinus fontinalis*) larvae could be reduced to 1.05 mg/L at 8°C. Complete survival of larvae was achieved at the approximate acclimation rate of 70 h per each 1.0 mg/L decrease in O_2 at 9°C; fish in Sinker Creek probably had a more gradual acclimation.

In the laboratory most fish species tend to move away from low DO areas and occupy higher locations in the water column (Kramer 1987), where DO is generally higher due to diffusion at the air-water interface. Early in the study redband trout were frequently seen swimming near the surface. As pool D shrank, most trout were observed in shallow water along the edge of the pool. Tramer (1977) observed Johnny darters (*Etheostoma nigrum*) lined up around pool margins with their heads facing outward in an oxygen-depleted pool. This position would provide easier access to the surface film where diffusion maintains higher levels of dissolved oxygen (Lewis 1970). The use of the surface film by fish is a response to low dissolved oxygen levels and is known as aquatic surface respiration (ASR, Lewis 1970). The ability to perform ASR is common among fishes living in hypoxia-prone waters (Kramer 1983), but it has not been reported for salmonids.

Shepard's (1955) observations of trout immediately surfacing upon the introduction of oxygen-deficient water to their tanks is the only evidence we could locate of salmonids performing ASR-type behavior. Gee et al. (1978) subjected rainbow trout, arctic char (*Salvelinus alpinus*), and lake whitefish (*Coregonus clupeaformis*) to progressive hypoxia, and none exhibited ASR behavior. They felt salmonids might not have evolved this behavior because they typically occupy well-oxygenated waters. Arid-land redband trout may be an exception (Behnke 1992).

A major factor enhancing redband trout survival was that as the pool shrank, the proportion of groundwater flow to surface water flow increased and air temperatures declined. Increased influence of groundwater and lower air temperatures reduced water temperatures, diel fluctuations in dissolved oxygen, and fish metabolic rates. Tramer (1977) found that fish mortality in isolated pools was highest during periods of maximum water temperature and diel DO fluctuation. Whitmore et al. (1960) observed juvenile chinook salmon (*O. tshawytscha*) strongly avoiding low DO (1.5–4.5 mg/L) areas in the summer when water temperatures were high but not in the autumn when water temperatures were cooler.

The ability of transplanted East Fork redband trout to survive in pool D was especially surprising. We initially expected that with their lack of acclimation to low DO levels, pool D would be lethal (Davis 1975). Although they appeared stressed initially, four of the six trout survived 43 days until perennial flow returned. Immediately upon being placed in pool D, these fish appeared to perform ASR. On subsequent visits they were usually seen lying along the pool margin partially covered by fallen leaves. Their breathing rate appeared relaxed and was much slower than when they were introduced into pool D.

Lowe et al. (1967) found greater survival of smaller-bodied native Arizona fishes in low oxygen concentrations than larger-bodied fishes. Shepard (1955), however, found that larger trout (12 g) tended to live longer at lethal DO levels than larval fish (1 g). In this study a large (146 mm, 60 g) redband trout outlived all small (<100 mm) redband trout in pool D, while just downstream in another pool of similar size eight small and no large redband trout survived (Vinson unpublished data). Speckled dace survived in high numbers in all pools until drying.

Although most of the redband trout died during our study, their ability to survive even a short time in these extreme habitat conditions, including our repeated electrofishing, which we feel may have been a source of delayed mortality, is noteworthy. The use of surface film water (ASR-type behavior) may be a strategy these fish use to survive periods of hypoxia in their harsh desert stream environment. Future study is needed to better describe the physiological tolerances of this desert fish species.

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FIELD STUDY OF PLANT SURVIVAL AS AFFECTED BY AMENDMENTS TO BENTONITE SPOIL

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ABSTRACT.—Efforts to reclaim amended and raw bentonite spoils with six plant species (two forbs, three shrubs, and one tree) were evaluated over a 4-year period. Plant species included fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.), big sagebrush (*Artemisia tridentata tridentata* Nutt.), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), Russian olive (*Elaeagnus angustifolia* L.), common yarrow (*Achillea millifolium* L.), and scarlet globemallow (*Sphaeralcea coccinea* [Pursh] Rydb.). Spoil treatments included addition of gypsum, sawdust, perlite, straw, and vermiculite; the control treatment was unamended. Fourwing saltbush had 52% survival across all spoil treatments, with greatest survival occurring on perlite-treated spoil (80%), followed by gypsum (70%) and vermiculite amendments (70%). Survival of other plant species ranged from 0 to 3% averaged across all treatments after 4 years. No differences in plant survival occurred among amendments when all species were considered.

Key words: shrubs, forbs, trees, Wyoming, mining, reclamation.

Bentonite, a montmorillonite clay, is a term referring to an altered deposit of volcanic ash (Barchardt 1977). In the northern Great Plains, bentonite is strip-mined from the Cretaceous marine Pierre and Mowry shale and Belle Fourche formations. Because of the spoils' saline sodic quality, high shrink-swell characteristics, limited internal drainage, arid and semiarid climate of the region, and absence of irrigation water, attempts at revegetation have faced restrictive problems (Hemmer et al. 1977, Bjugstad 1979).

In the absence of drainage and leveling possibilities, Russell (1973) suggested the planting of salt-tolerant *Atriplex* species. Voorhees et al. (1987) reported successful growth of rillscale (*A. suckleyi* [Torrey] Rydb.), a native annual, on bentonite mine spoil with amendments and supported use of this species for early revegetation on such spoils. Nutritional qualities of rillscale are generally adequate for livestock and wildlife (Voorhees 1990). Sieg et al. (1983) also reported that rillscale was the most successful invader of bentonite-mined land spoil in southeastern Montana. Other investigators using various species of plants (Hemmer et al. 1977, Bjugstad 1979, Dollhopf et al. 1980, Dollhopf and Bauman 1981, Smith et al. 1985, 1986, Voorhees et al. 1987) have reported varying degrees of success on bentonite mine spoils using topsoil and spoil amendments to promote growth and establishment of plants. However, with the limited quality and quantity of topsoil on shale overburden of bentonite mine lands, a realistic and practical approach is to use salt- and drought-tolerant plants (Shannon 1979), fertilizers, and both organic and chemical amendments on raw spoils. Organic and chemical amendments are primarily intended to promote development and aggregation of the spoil material and to ameliorate the dispersion effect of excessive sodium.

In an earlier greenhouse study, Uresk and Yamamoto (1986) showed that salt- or drought-tolerant plants can survive in amended or untreated bentonite mine spoil. The objective of this study was to obtain field verification of the greenhouse study and to test effects of amendments on raw bentonite mine spoil for survival of salt- and drought-tolerant plants.

MATERIALS AND METHODS

Study plots are located near Upton, Wyoming, on property owned by the American Colloid Company. Average precipitation is 380 mm per year, with highest rainfall occurring during the period from May through July. Average annual air temperature is 6°C, with an average low of –17°C in January and an average high of 23°C in July. The climate can be characterized as dry, hot, and windy in the summer and windy and cold in the winter. Stands of ponderosa pine (*Pinus ponderosa* Laws.) and sagebrush (*Artemisia*)/grass vegetation characterize areas around the bentonite mines. Bentonite mine spoils are essentially derived from the Mowry shale formation. Study plot surfaces were barren with 15 cm of loose shale spoil or exposed Mowry shale beds. These shale spoils are extremely hard and crusty when dry. Mowry shale is classed as siliceous shale (Pettijohn 1957), with an abnormally high silica content of 85% vs. 58% for normal shales. Its siliceous character is attributed to its volcanic ash origin (Rubey 1929).

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Uresk and Yamamoto (1986) previously reported on the spoil properties (0–20 cm sampling depth) of the study site. Spoil is adequate in NPK status with nitrate nitrogen at 19 kg/ha, ammonia-nitrogen at 55 kg/ha, phosphorus and potassium at 39 μg/g and 170 μg/g, respectively. Soluble salt concentrations vary markedly, but the spoils are saline (EC of 9.2 mmhos/cm) and sodic (SAR 33.1). Spoil pH averaged 6.9 but ranged from 4.1 to 8.0. X-ray diffraction of bentonite spoil revealed a mixture of silicate clay types with a dominance of illite based on the CEC of 30 meq/100g, rather than montmorillonite as sometimes believed (Uresk and Yamamoto 1986). Other clays included montmorillonite and kaolinite. Additional information on chemical characteristics of raw bentonite spoil from the study area is reported by Voorhees et al. (1987).

Five different amendments to raw spoil materials were applied in 1979 (Table 1). Four spoil treatments included ponderosa pine sawdust, wheat straw, perlite, and vermiculite. Fertilizer (NPK, 11-5-6) was added at 84 kg/ha to all treatments except the control. Additional nitrogen (dry pellet) was added to sawdust and straw spoil treatments at 12 kg/mt and 8 kg/mt, respectively, at time of planting. Each amendment was mixed with bentonite spoil at a 50:50 volume ratio with added gypsum at 10 mt/ha-30 cm depth. The fifth treatment, without any physical amendment, was gypsum at 20 mt/ha-30 cm depth (USSLS 1954). The sixth treatment was a control (untreated). All treatments except the control were surface mulched with ponderosa pine woodchips to a depth of 2 cm.

Six plant species were selected on the basis of drought and saline-alkali tolerance (Gill 1949, Wright and Bretz 1949, McKell 1978): fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.), big sagebrush (*Artemisia tridentata tridentata* Nutt.), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), Russian olive (*Elaeagnus angustifolia* L.), common yarrow (*Achillea millifolium* L.), and scarlet globemallow (*Sphaeralcea coccinea* [Pursh] Rydb.). Russian olive and Rocky Mountain juniper were 3- and 1 1/2-year-old bare root seedlings, respectively; the remaining species were 1-year-old container-grown seedlings. All plants were planted in mid-May 1979. Survival of plants was evaluated twice per year (spring and fall) from 1979 to 1982.

The experimental design was a 6 × 6 (6 species × 6 treatments) factorial arrangement with two replications accomplished through randomized blocks. Each block consisted of 6 treatments (columns) per species with 10 plants per treatment. Twenty plants for each species were evaluated per treatment in this design. Plants were spaced 1 m apart, within and between columns. Each plant was planted

TABLE 1. Experimental design with six treatments and added supplements.

	Treatments					
Supplements	Control[1]	Gypsum	Sawdust	Perlite	Straw	Vermiculite
NPK(11-5-6) 84 kg/ha		X	X	X	X	X
N			12 kg/mt		8 kg/mt	
Gypsum (10 mt/ha-30 cm depth)		X	X	X	X	X
Mulch (2 cm depth)		X	X	X	X	X

[1] Raw bentonite spoil only

to the depth of the root crown in a hole 30 cm in diameter and 35 cm deep with the bottom 5 cm filled with sawdust. The hole was then backfilled with spoil, chemical and physical amendments. Each plant was gently watered (deionized tap water) to saturation immediately after planting. The study site was visited once a week for watering (1 L per plant) during the first month after transplanting and biweekly thereafter from May to September for two growing seasons (1979 and 1980).

Differences in survival among species and treatments were analyzed by chi-square procedures for comparison of proportions from many samples (Fleiss 1973). All differences were evaluated at $\alpha = .10$.

RESULTS AND DISCUSSION

Mortality of all plant species was very high after the first growing season. All Russian olives died after 2 weeks, and further documentation of this species was discontinued. (1) Survival and growth of these species on field plots of bentonite spoil was different from that recorded in the greenhouse (Uresk and Yamamoto 1986). (2) Fourwing saltbush performed well, with an overall survival rate of 52% after four growing seasons (Table 2). Survival rate for this species was greatest on the perlite spoil amendment (80%) followed by gypsum (70%) and vermiculite (70%) amendments. Survival of yarrow, scarlet globemallow, and big sagebrush was very low but did indicate some adaptability to amended spoils.

The halophytic capabilities of many members of the genus *Atriplex* are well documented in literature (Waisel 1972, Osmond et al. 1980, Richardson and McKell 1980, Tiedemann et al. 1984). A 40% survival of fourwing saltbush on the control treatment (Table 2) demonstrates the natural adaptability of this species to saline-alkali conditions. Survival rates increased 40 percentage units when the perlite amendment was utilized. Gypsum and vermiculite showed survival rates increased 30 percentage units but were not significantly different from the control. This indicated that some gains in survival could be attained by amendment of raw bentonite spoil, although not significant at $P = .10$. In this study overall plant survival was greatest with perlite.

Adding sawdust has been the most accepted amendment for reclaiming raw bentonite spoils; however, there are differences in opinion on the desirability of using sawdust. It has shown some beneficial results, particularly when applied as mulch and eventually worked into the soil (Lunt 1955). Others have tried applying sawdust or shavings to their soils with disappointing and sometimes disastrous results (Lunt 1955). Most researchers have observed no toxicity when adequate nitrogen was used with sawdust or other wood products (Allison and Anderson 1951). However, tannins, resins, and secondary compounds

TABLE 2. Survival of transplanted plant species in bentonite mine spoil treatments after four growing seasons at Upton, Wyoming.

Species	Spoil treatment						
	Control (%)	Gypsum (%)	Sawdust (%)	Perlite (%)	Straw (%)	Vermiculite (%)	Average survival[1] (%)
Yarrow	0	0	15	5	0	0	3^{a}
Rabbitbrush	0	0	0	0	0	0	0^{a}
Scarlet globemallow	0	0	0	0	0	5	1^{a}
Fourwing saltbush	40^{ab}	70^{ab}	30^{ab}	80^{b}	20^{a}	70^{ab}	52^{b}
Big sagebrush	0	0	0	10	10	0	3^{a}
Rocky Mountain juniper	0	0	0	0	0	0	0^{a}
Average survival	7^{a}	12^{a}	8^{a}	16^{a}	5^{a}	13^{a}	10

[1] Means in row or column followed by the same letter are not different at $\alpha = .10$. Absence of letters indicates no statistical significance.

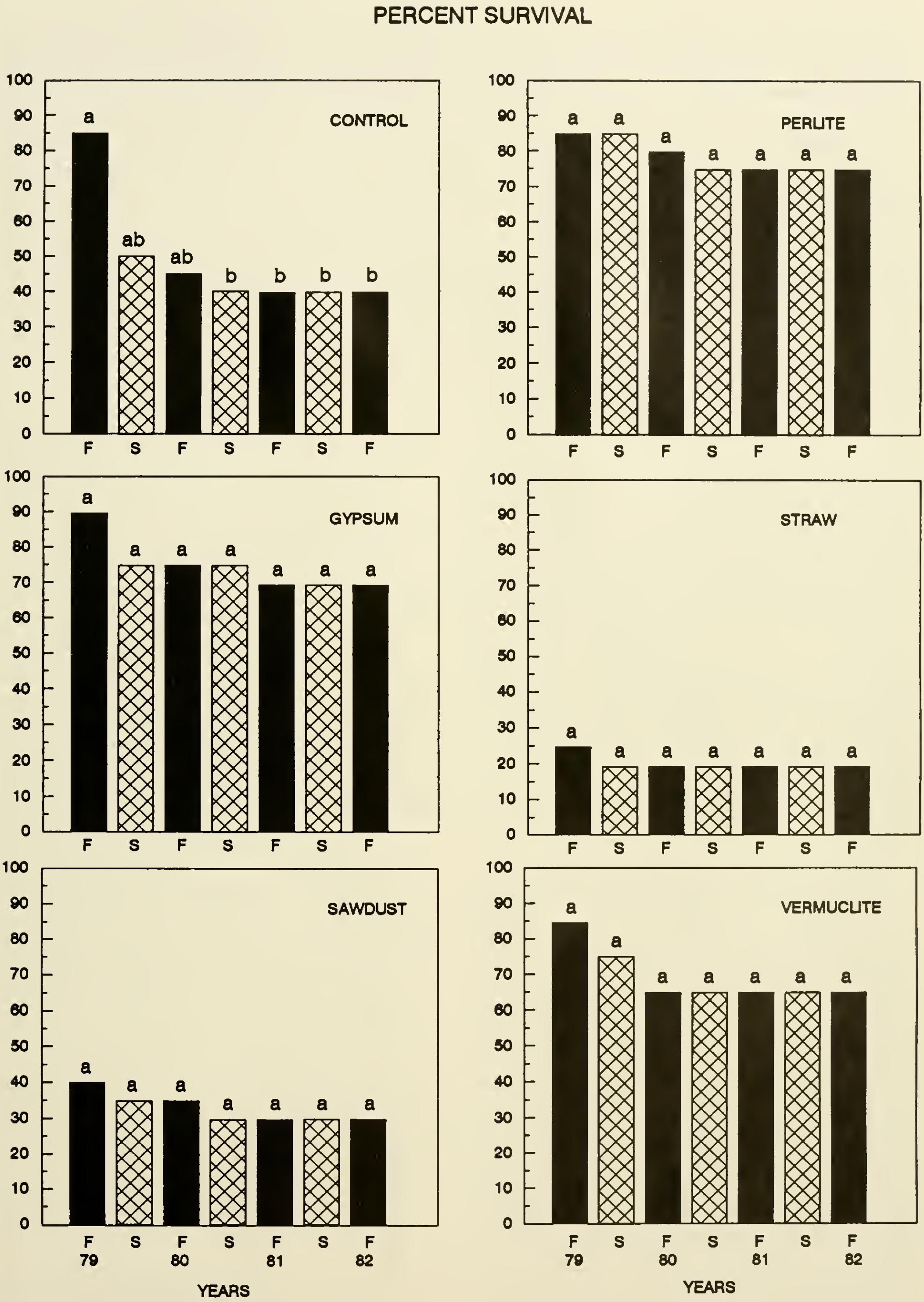

Fig. 1. Survival of fourwing saltbush during fall (F) and spring (S) measurements, 1979–82, at $\alpha=.10$.

from fresh sawdust are possibly toxic to plants. Also, increased soil acidity from sawdust may decrease survival (Allison and Anderson 1951). Sawdust added to raw bentonite spoils increased water infiltration (Voorhees 1986). Infiltration rates have not been evaluated against perlite or vermiculite as amendments. In addition, Voorhees et al. (1987, 1991) and Voorhees and Uresk (1990) found that bentonite spoil amended with sawdust, alone or in combination with other amendments, increased growth of rillscale through two growing seasons. Schuman and Sedbrook (1984), Smith et al. (1985), and Belden et al. (1990) showed that sawdust added to spoil, with wood chips added to the surface, promoted vegetation establishment over a 4-year period.

Measurements of spoil pH from the fourwing saltbush plots after four growing seasons ranged from 6.1 to 6.8 for the various treatments. These values were generally 1–2 units lower than pH values of bentonite spoils measured at the termination of the greenhouse study (Uresk and Yamamoto 1986). Lowest pH values were found in samples from plots that had been amended with sawdust, straw, or vermiculite. Since vermiculite amendment was associated with higher survival trends of fourwing saltbush, and sawdust and straw amendments with the lowest survival, pH may not have been a factor in survival of fourwing saltbush.

Examination of survival for fourwing saltbush (Fig. 1) showed that greatest mortality for all treatments except the control occurred during the first growing season prior to fall evaluation. Thereafter, no significant mortality occurred, except on the control treatment. Greatest survival rates of fourwing saltbush were with perlite, vermiculite, and gypsum. These materials and their mixes are well known in plant nurseries and in the horticultural industry as pot mixes. Apparently, they mix well with bentonite spoils, improve plant survival rates, and may indicate that water infiltration, aeration, and bulk density characteristics are improved with their addition to spoils.

With the exclusion of fourwing saltbush, overall average survival rates of selected plant species across amendment-treated spoils after four growing seasons were 0–3%. Fourwing saltbush demonstrated a natural adaptability to establishment on saline-alkali bentonite spoil, with an overall survival rate of 52%. Perlite, vermiculite, and gypsum amendments enhanced survival rates for fourwing saltbush. Sawdust and straw amendments did not increase survival as much as perlite or vermiculite amendments, but plant survival on these amendments was very stable. Sawdust and straw are materials that are readily available in the Black Hills and in bentonite mining areas. Further experimentation with differing rates, type of applications, bed preparations, and times of planting and seeding are needed, especially for shrubs and forbs.

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POPULATION STRUCTURE AND ECOLOGICAL EFFECTS OF THE CRAYFISH *PACIFASTACUS LENIUSCULUS* IN CASTLE LAKE, CALIFORNIA

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and Charles R. Goldman[2]

ABSTRACT.—The recent appearance of the "California crayfish," *Pacifastacus leniusculus*, in Castle Lake, California, and interest in its potential impacts on the lake ecosystem provided motivation for a study of the population structure and habitat use of this species and its effects on aquatic macrophytes. Mark-recapture studies indicated that the total number of adult (3^+ yr or older) crayfish in the lake was ca 10,100 individuals, yielding an estimate of lakewide crayfish density in preferred crayfish habitats of 0.13 adults m^{-2}. Using mean body mass of individuals, we estimated that ambient biomass density was 5.9 g m^{-2}. Length-weight relationships determined for captured individuals were sex dependent, with males having greater body mass for a given carapace length. Length-frequency and weight-frequency diagrams indicated that *P. leniusculus* reaches larger sizes in Castle Lake than do populations of *P. leniusculus* in ultraoligotrophic Lake Tahoe. Population-wide, males were significantly larger in both carapace length and body mass than females. We also examined sex dependence of interhabitat differences in crayfish body size by comparing animals trapped in rocky areas with those from areas with macrophytes and soft sediments. No significant differences in overall body size were found between habitats, but a significant habitat-sex interaction term occurred because the sex-dependent size differences were more pronounced in sediment than in rocky areas. Exclosure and enclosure experiments indicated that crayfish had large but differential impacts on Castle Lake macrophyte species, as the abundance of two of the dominant species (*Chara* sp., *Potamogeton richardsonii*) declined in the presence of crayfish and, in one case, increased in exclosures. These effects occurred via both consumptive and nonconsumptive mechanisms. These studies indicate that an expanding population of *P. leniusculus* in Castle Lake may be producing sizable impacts on the littoral zone habitat.

Key words: crayfish, herbivory, macrophytes, Pacifastacus leniusculus.

Littoral zones are important to the dynamics of lake ecosystems (Wetzel 1983, Carpenter and Lodge 1986). Vascular plant communities (macrophytes) are particularly important in the littoral zone, providing food resources for herbivores, attachment substrata for periphyton, and cover for both predators and prey. Macrophytes are also particularly important in fueling detritus food chains (Wetzel 1983). Traditionally, studies have generally emphasized the influence of physical (e.g., light availability or wave action; Spence 1982) and chemical (inorganic carbon; Sand-Jensen 1978) factors in regulating littoral zone macrophyte communities; as a result, biotic interactions, particularly herbivory, have been considered less important (Gregory 1983, Wetzel 1983).

However, recent experimental studies indicate that invertebrate and vertebrate herbivores can have large impacts on macrophytes and that herbivory impacts vary for different macrophyte species (Lodge 1991). Crayfish may be particularly important in influencing the dynamics of littoral zone plant communities because of their diverse feeding modes; crayfish may act as predators (consuming other littoral zone invertebrates), as herbivores, or as detritivores. Past studies of crayfish impacts on macrophytes indicate that their effects occur directly (via both consumptive and nonconsumptive mortality; Lodge and Lorman 1987) as well as indirectly via predation on other potential herbivores (Hanson et al. 1990). However, only a few of the 11 genera and 300 named species and subspecies of crayfish in North America (Bouchard 1978) have been studied with respect to their potential impacts on littoral zone vegetation.

The "California crayfish," *Pacifastacus leniusculus*, is a member of family Astacidae and includes three subspecies with a range that encompasses northern California and much of the Pacific Northwest (Miller 1960).

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Abrahamsson and Goldman (1970) suggested that *P. leniusculus*, introduced to Lake Tahoe at the turn of the century, were important in determining the distribution of macrophyte communities at depths less than 50 m. Flint and Goldman (1975) subsequently supported this suggestion experimentally, showing that *P. leniusculus* controlled *Myriophyllum* at shallow depths. Flint and Goldman also demonstrated that low levels of crayfish grazing enhanced primary productivity by attached algae.

In 1988 researchers observed individuals of *P. leniusculus* in the littoral zone of Castle Lake, where it had been unrecorded previously during nearly 30 years of ecological research (Beatty 1968, Swift 1968, Neame 1975, Carlton 1982, Paulsen 1987, Hagley 1988). Therefore, in the summer of 1990 we began studies designed to evaluate population size and structure, habitat utilization, and potential effects on macrophyte communities of *P. leniusculus* in this subalpine lake.

MATERIALS AND METHODS

Study Site

Castle Lake is a relatively small (20 ha) but deep (35 m maximum depth) subalpine lake located in the Siskiyou Mountains of northern California (Siskiyou County), USA (41°13′N, 122°22′W). The main basin of the lake is relatively steep sided, but the lake contains an extensive shallow (<4 m) shelf on its northeast side. Bottom substrates are diverse and include steep-sided rock faces and boulders in the vicinity of the lake's cirque face, coarse particulate–dominated sediments in the vicinity of forested slopes, and flocculent, low-density organic sediments that cover most of the bottom of the main basin below depths of 10 m as well as much of the shallow shelf. According to recent work of Hagley (1988), the most abundant macrophyte species of Castle Lake are *Isoetes occidentalis* (Henders.), *Chara* sp., and *Potamogeton* sp. (*P. richardsonii* [(Benn.) Rydb.] is dominant but *P. gramineus* [L.] is also present.)

Population Estimates

Estimates of crayfish population abundance were made via the multiple-recapture Schnabel method (Schnabel 1938), with capturing, marking, releasing, and resampling of animals occurring at biweekly intervals from July through mid-September 1990. Animals were captured using cylindrical nylon-mesh traps with funneled entrances and baited with dead fish. Traps were set overnight in shallow waters (<10 m) in all areas of the lake in late afternoon or early evening and retrieved in early morning. To estimate depth distribution of crayfish in the Castle Lake littoral zone, on five occasions we established transect trap lines across the depth contours of the lake to determine the maximum depths at which crayfish could be found; each transect sample consisted of 15 traps placed at 10-m intervals along a nylon line. These extended to a depth of ca 25–30 m. Sex, carapace length, and wet weight of each animal were recorded. Animals were also classified with respect to areas from which they were obtained, i.e., rocky bottoms vs. those with organic sediments. All large animals (generally >35 mm carapace length [CL], age 3^+ yr according to Abrahamsson and Goldman [1970], although similarly sized individuals in Castle Lake may be younger than those growing in ultraoligotrophic Lake Tahoe) were given unique marks via cauterization of the carapace (Abrahamsson 1965) and returned to the lake. We rarely captured recently moulted crayfish, indicating that the majority of moulting had occurred prior to our sampling period. Thus, our results are not likely to be complicated by potential changes in trapability in response to moulting events. A total of 750 animals were eventually marked during the sampling period.

Exclosure/Enclosure Studies of the Effects of *P. leniusculus* on Macrophytes

To examine potential ecological effects of crayfish on the macrophyte communities of Castle Lake, we performed an 8-wk exclosure/enclosure experiment. Cages consisted of 1 × 1 × 1-m wood-framed cages covered with 0.9-cm mesh nylon netting on sides and top. Replicate (n = 4) enclosures received either one or three adult male crayfish (50–52 mm carapace length, ca 47 g body weight), equivalent to densities of 47 g m^{-2} and 141 g m^{-2}, respectively. Adult crayfish were used because earlier studies suggested that smaller crayfish tend to be more carnivorous than herbivorous, while adults are usually primarily herbivorous

(Abrahamsson 1966). Logistical constraints on the size of enclosures we could use meant that enclosure densities were likely higher than ambient crayfish densities (see Results). Thus, we also decided to maintain four exclosures that received no additions of crayfish and were inspected to ensure that no animals had been enclosed. Results of exclosure treatments thus are critical in assessing whether potential herbivore impacts detected in enclosures with artificially high animal densities are likely to be operating in the lake itself. Support for the hypothesis that crayfish are exerting an impact on macrophytes in the lake itself would come not only from depressed biomass of macrophytes in enclosure treatments but more importantly from increases in macrophyte biomass in exclosures where macrophytes are protected from ambient grazing intensity. When each exclosure or enclosure was positioned, a control section of equal area was also delineated to be sampled at the end of the experiment to enhance the power of statistical analyses. Without paired control areas, high site-to-site variation in local macrophyte abundance might overwhelm treatment effects even if treatments substantially altered local macrophyte abundance. Thus, a total of eight enclosures and four exclosures, each with a paired control area, were monitored.

Cages, with control areas, were placed along the 3–5-m contour interval within vegetated areas of the lake. Cages were checked at weekly intervals via scuba, and crayfish were added to enclosures from which animals had escaped (this happened twice); no crayfish were observed inside exclosures. At the end of the 8-wk period, the above-sediment portions of all submersed macrophytes in each cage and control area were harvested, sorted by species, drained, and weighed to the nearest gram.

RESULTS AND DISCUSSION

The estimated population size of adult *P. leniusculus* (i.e., individuals ≥ 3 yr) in Castle Lake obtained using the Schnabel method was 10,100 ± 23 (SD) individuals. Our trap transects across depth contours in the lake indicated that crayfish did not generally inhabit bottom areas below 10 m, as at these depths the bottom is dominated by soft, flocculent sediments. Likewise, animals were rarely caught in traps placed in much of the shallow shelf area of the lake, which is also dominated by soft sediments lacking macrophyte development. Thus, we then estimated the total amount of crayfish habitat as the total bottom area shallower than 10 m (117,000 m^2) minus the estimated area of the shallow shelf dominated by soft sediments (ca 42,400 m^2), yielding a total habitat area of ca 74,600 m^2. Thus, average crayfish densities in Castle Lake were approximately 0.13 adults m^{-2}. This estimate is somewhat lower than, for example, the estimates of densities of *P. leniusculus* made by scuba census and trapping efficiency in ultra-oligotrophic Lake Tahoe (0.16–5.85 adults m^{-2}) and oligotrophic Donner Lake (0.23–0.44 adults m^{-2}) reported by Abrahamsson and Goldman (1970), Flint and Goldman (1977), and Goldman and Rundquist (1977). Some of this discrepancy may reflect differences in methodology (mark-recapture, which focused only on adults, vs. scuba census or trapping efficiency methods, which included juvenile animals). In addition, our estimate is likely to be on the low side as we conservatively included bottom areas down to 10 m although our transect data indicate that a majority of catches were made at depths shallower than 5 m. Therefore densities in the habitat areas predominantly used by *P. leniusculus* in Castle Lake are likely higher and likely approach the lower end of the range reported for Lake Tahoe (ca 0.2 adults m^{-2}).

By stratifying the population estimates based on relative catches in different parts of the lake, we estimated populations of 8000 individuals in rocky-bottomed areas of the lake and 2100 in macrophyte-dominated areas. Average body mass (male and female) of sampled crayfish was 45.6 g, and therefore areal biomass of crayfish in Castle Lake was 5.9 g m^{-2}. The sex ratio for animals in all catches was 0.90 (female:male).

Length and wet-weight measurements were made on approximately 1188 animals during the course of the sampling season. Length-weight relationships differed significantly for males and females (based on confidence limits on the slopes of the length-weight relationships), with males having greater body mass for a given carapace length, especially at larger sizes (Fig. 1). This may reflect the fact that male chelae undergo allometric growth during ontogeny, while female

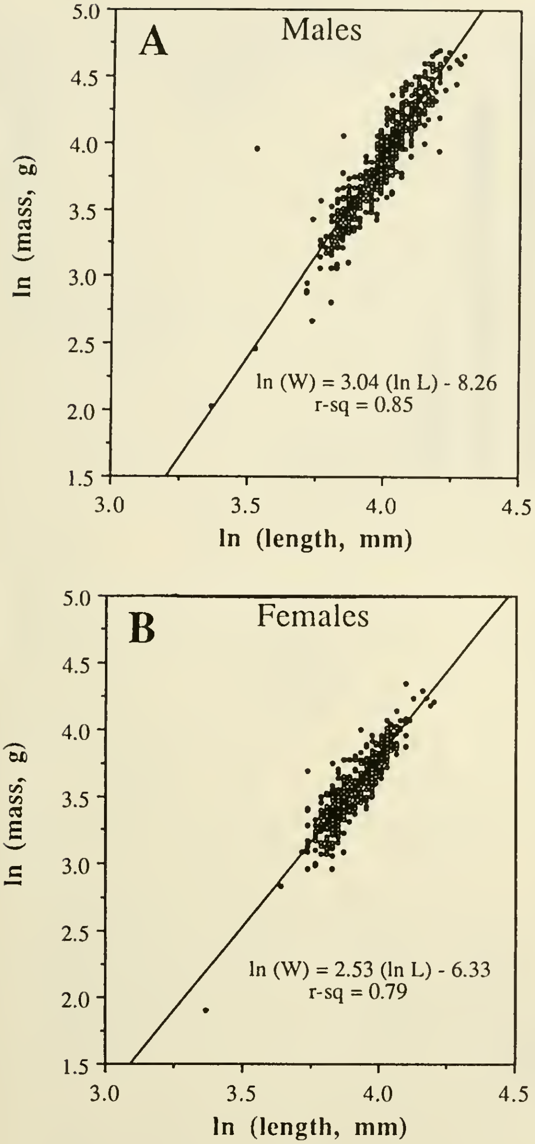

Fig. 1. Length–wet weight relationships for male (A) and female (B) crayfish. Allometric relationships fit to the data are given.

chelae grow isometrically (Mason 1975). In addition, males were on the whole larger in carapace length (and body mass) than females ($P < .05$ based on a t test; Fig. 2), possibly reflecting the fact that females must necessarily invest substantial portions of their energy budgets in reproductive output. The size frequency distribution (Fig. 2) was quite broad, with largest individuals reaching 70^+ mm CL. This contrasts with the results of the studies by Abrahamsson and Goldman (1970) and Flint (1975) of *P. leniusculus* in ultraoligotrophic Lake Tahoe, where the largest animals observed were around 55 mm CL. Without more detailed sampling and cohort analyses it is not possible to determine whether this difference reflects faster growth rates or longer life span in Castle Lake relative to Lake Tahoe.

We also used ANOVA to compare male and female sizes in different habitat categories (rocky vs. sediment/macrophyte areas; Fig. 3). While there was no significant main effect of habitat type on crayfish body size, there was a significant habitat × sex interaction, as male body size in sediment/macrophyte areas was higher than in rocky areas, with the opposite being true for female crayfish. It is important to note that baited traps are biased in favor of large males (Brown and Brewis 1978); thus, interpretation of data on sex-dependent differences in body size between habitats is complicated by the possibility that trap bias operates differently at different locations. Bearing this in mind, the patterns illustrated in Figure 3 may reflect interacting influences of burrow availability in different habitats and size- and sex-dependent dominance patterns between individual crayfish. Behavioral studies of *P. leniusculus* are limited, but the study of Momot and Leering (1986) indicated that, within sexes, large *P. leniusculus* are dominant over small but that, for animals of the same size, females dominate over males. Given this suggestion and our lack of knowledge about general burrow availability in different bottom types in Castle Lake, we can only speculate about the factors contributing to observed sex-dependent differences in body size between habitat types. It is possible, for example, that general burrow shortages in sediment regions cause these regions to be dominated by the largest (and therefore most dominant) male crayfish able to successfully defend the limited number of available burrows, resulting in a larger mean body size for males in sediment areas. However, the observation that the opposite pattern was true for females (females tended to be larger in rocky areas than in sediment areas) suggests that simple dominance patterns and general burrow shortages are insufficient to explain these data, as it is possible, for example, that the quality of available burrows may be different for females than for males. Experimental studies of burrow choice

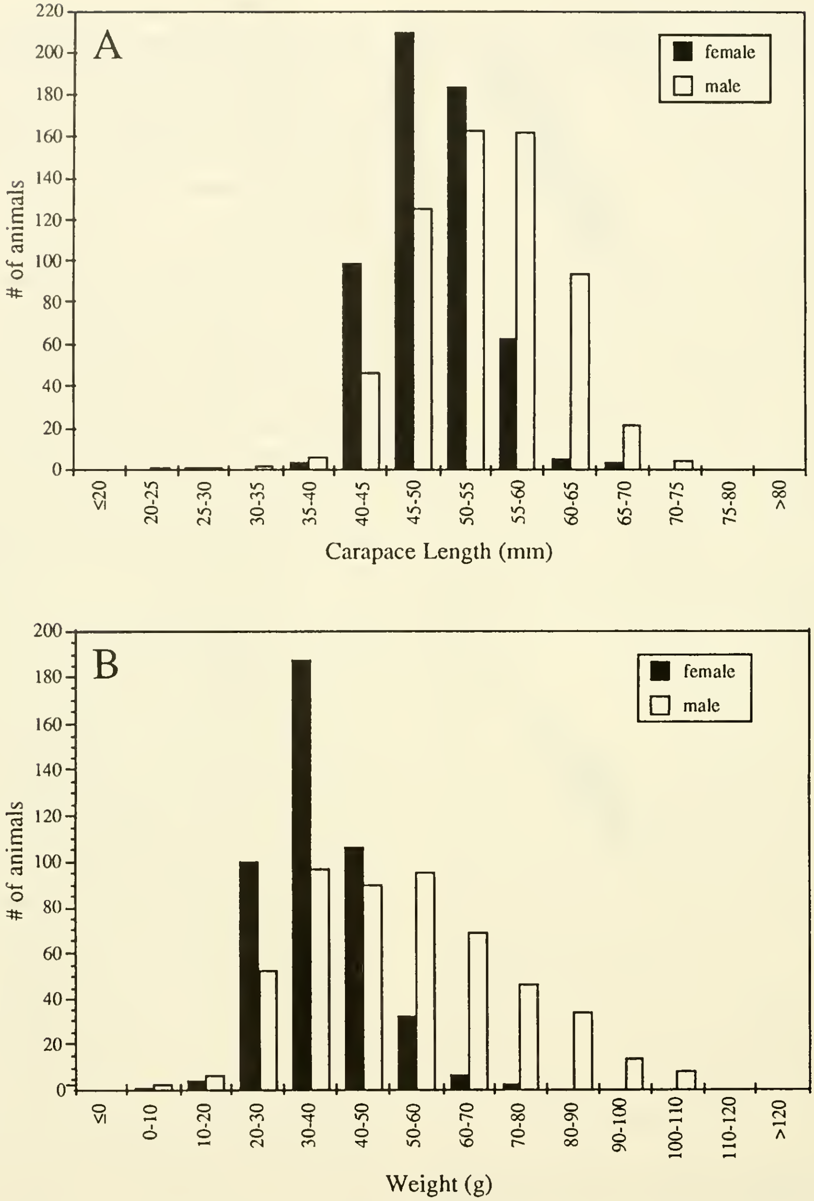

Fig. 2. Length-frequency (A) and weight-frequency (B) diagrams for male and female crayfish. Males were significantly ($P < .05$) larger and heavier than females.

and defense and aggressive displacement in different habitats, as well as the sex-dependence of these phenomena, are needed to elaborate on these possibilities.

Our enclosure/exclosure experiment indicates that *P. leniusculus* exerts substantial grazing pressure on the aquatic macrophytes of Castle Lake, as both total biomass and biomass of certain species responded to the presence or absence of crayfish (Fig. 4). However, densities of crayfish used in the experimental enclosures (one or three adult male crayfish per square-meter enclosure) exceeded our estimates of ambient densities of adult crayfish in the lake (ca 0.15–0.20 crayfish m^{-2}) by more than fivefold. High densities of crayfish in enclosures were the necessary result of having to construct enclosures of manageable size that would not disturb, or be disturbed by, other human users of the lake. The observation

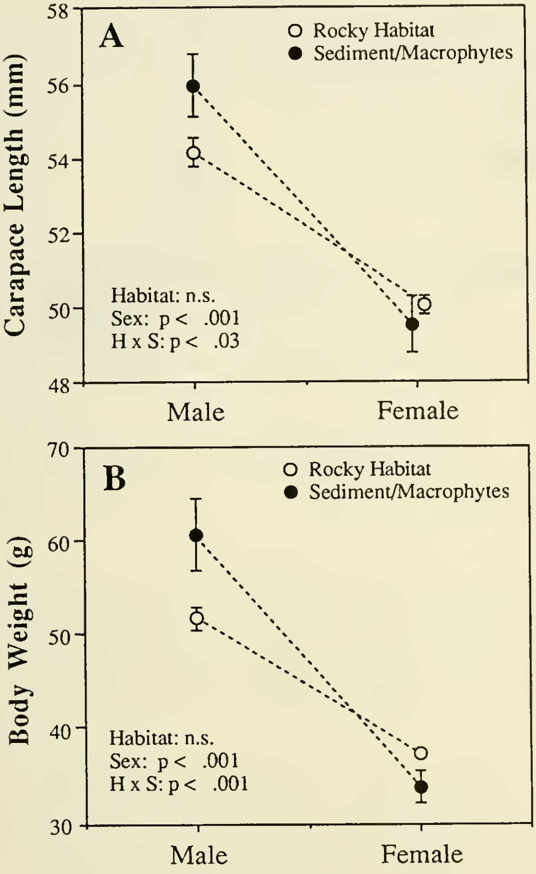

Fig. 3. Body size of male and female crayfish in different habitat types: A, carapace length; B, body weight. Analysis of variance indicated no significant main effect of habitat on animal size, but there was a significant habitat-sex interaction ($P < .001$), reflecting a pronounced difference between habitats in males but an opposite, and lesser, difference for females. Error bars represent ±1 SE for each mean.

that crayfish impacts did not increase in three- vs. one-crayfish treatments suggests that the artificially high crayfish densities in enclosures created unrealistic intensities of herbivory. Thus, the potential exists that reductions in macrophytes relative to control areas reflect these artificially high levels of crayfish and that crayfish grazing at ambient levels is inconsequential for macrophytes. However, this conclusion is not supported by the observation that macrophyte biomass increased greatly in exclosures, which prevent ambient crayfish grazing, relative to control areas exposed to crayfish. *Chara* biomass increased in the enclosure treatment by a factor even greater than its decline in the exclosure treatments, consistent with our prediction that, if crayfish grazing is important under natural lake conditions, macrophyte biomass should increase strongly when ambient grazers are excluded. We also observed that *Chara* canopies in experimental exclosures were more branched, taller, and more open than *Chara* stands in both the crayfish enclosures and the lake itself, suggesting that crayfish grazing is important in the natural lake condition, a conclusion supported by our observation during nighttime scuba dives that most of the observable crayfish could be found feeding on the *Chara* beds.

The impact of *P. leniusculus* on macrophytes was clearly species dependent. No effect of either exclosures or enclosures was observed for *Isoetes*, a pteridiophyte with relatively tough leaves arranged in a basal rosette. No statistically significant impacts were detected for *Potamogeton* either. However, these results are misleading, as they are largely an artifact of the general scarcity of *Potamogeton* in the Castle Lake littoral zone. This scarcity resulted in a poor representation of *Potamogeton* among experimental treatments (only one exclosure and a single one-crayfish enclosure had *Potamogeton* initially *and* in the adjacent control area). In fact, in all four cases where *Potamogeton* occurred in enclosures with crayfish, abundance was reduced to zero as crayfish snipped off the single-stemmed plants at the base. This example of nonconsumptive mortality is similar to that observed by Lodge and Lorman (1987) for *Orconectes rusticus* feeding on *Megalodonta beckii* and *Vallisneria americana.* The impact of such whole-plant mortality is undoubtedly more extreme in its impact than partial consumption of individual plant parts and may account for the general scarcity of *Potamogeton* in Castle Lake. The low impact of *P. leniusculus* on *Isoetes* may reflect the low potential food values of this species. Hagley (1988) reports a high C:N ratio for *Isoetes* in Castle Lake (ca 14–18:1 by weight vs. 10–11:1 for *Chara* and *Potamogeton* vegetative shoots); low C:N ratios in plant materials are generally considered indicative of nutritionally superior foods for a wide variety of herbivores (Mattson 1980, Crawley 1983).

Biomass of the macroalga *Chara* changed significantly in both exclosures and enclosures. This response reflects consumptive grazing by crayfish, as we never saw severed *Chara* "stems" inside crayfish enclosures. The

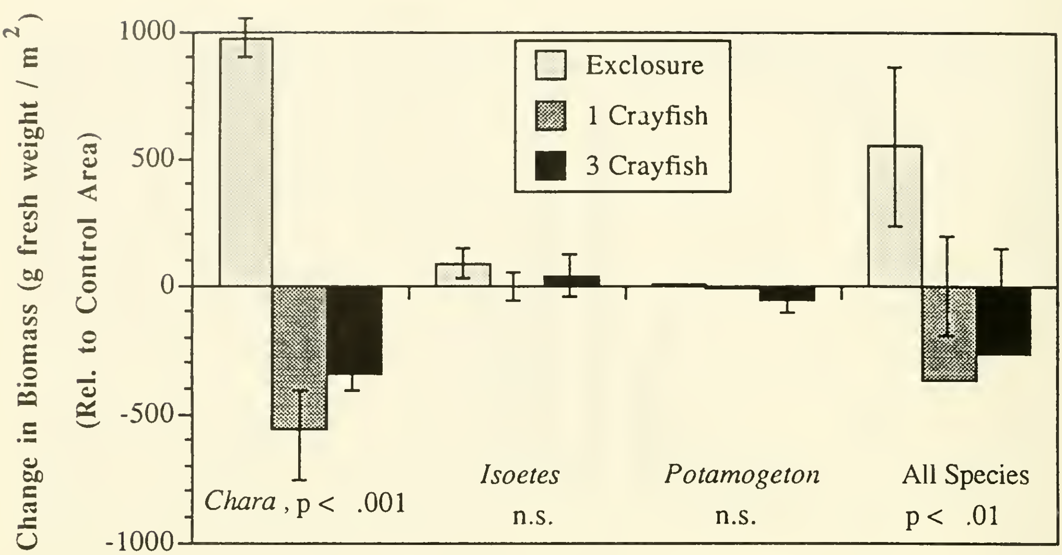

Fig. 4. Results of crayfish exclosure/enclosure experiments. Analysis of variance indicated the presence of crayfish had significant effects on total macrophyte abundance ($P < .01$) and on *Chara* ($P < .001$). Although *Potamogeton* was nonconsumptively eliminated in all enclosures in which it occurred with crayfish, no statistically significant effect was observed for *Potamogeton*, largely a result of poor representation of this species among experimental units. *Isoetes* was unaffected by crayfish. Error bars represent ±1 SE for each mean. Error bars are missing for the exclosure and one-crayfish treatments for *Potamogeton* because *Potamogeton* was present in both treatment and control areas in only one replicate pair for these treatments.

substantial and rapid increase in *Chara* biomass in exclosures indicates that crayfish potentially regulate the natural abundance of *Chara* in Castle Lake; high *Chara* growth rates may permit it to persist in the face of this consumption. Overall distributions of these macrophytes are consistent with the differential impacts of crayfish just described: *Isoetes* dominates bottom areas with large crayfish populations while *Potamogeton* is confined to sediment-dominated littoral zone areas where crayfish abundance is lowest. In sum, our observations of the abilities of *Pacifastacus leniusculus* to differentially regulate macrophyte species in this lake lend further support to the conclusions of Lodge (1991) that macrophytes are actively engaged in aquatic food webs via direct consumption by herbivores, in addition to their role as contributors to detrital-based trophic pathways.

Given the potential influences of crayfish-induced mortality on Castle Lake macrophytes demonstrated by the cage experiments, it would be of interest to know the history of the *P. leniusculus* population in this system. Previous thorough investigations of the Castle Lake littoral zone do not report any crayfish. However, crayfish carapaces were observed in the lake as early as 1986 (E. Marzolf personal communication), and a substantial population was verified during gill net studies of Castle Lake rainbow trout begun in 1988. This places the date of potential introduction of crayfish in the mid-1980s, as a considerable amount of littoral zone research occurred in Castle Lake in the early 1980s with no report of crayfish (e.g., Paulsen 1987, Hagley 1988). In the absence of a more thorough evaluation of present-day species composition, spatial distribution, and biomass development of Castle Lake macrophytes, it is not possible to evaluate whether these assemblages changed during the period between the macrophyte studies of Hagley (1988) prior to crayfish introduction and 1990 when our study was performed. However, given that invasions of new species into unoccupied habitats are often explosive, population densities of *P. leniusculus* in Castle Lake may increase even further and approach those densities actually used in our experimental enclosures; this possibility is supported by recent (1992–93) crayfish trapping, which indicates that catch-per-unit-effort may have increased by a factor of 2–3 since our 1990 study (J. J. Elser personal observation). Thus, our experimental studies likely yield some insights into the impacts on macrophytes of further population development of *P. leniusculus*, providing an additional illustration of the effects of invading species on aquatic ecosystems.

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BROOD HABITAT USE BY SAGE GROUSE IN OREGON

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ABSTRACT.—Habitat use by Sage Grouse (*Centrocercus urophasianus*) hens with broods was examined at Jackass Creek and Hart Mountain, Oregon, from 1989 through 1991. Sage Grouse hens initially selected low sagebrush (*Artemisia* spp.) cover types during early brood-rearing, big sagebrush cover types later in the brood-rearing period, and ultimately concentrated use in and near lakebeds and meadows. Areas used by Sage Grouse broods typically had greater forb frequency than did random sites. Hens at Jackass Creek selected sites with forb cover similar to that generally available to broods at Hart Mountain, but home ranges were larger at Jackass Creek because of lower availability of suitable brood-rearing habitat. Differences in habitat use by broods on the two areas were reflected in dietary differences; at Hart Mountain, chicks primarily ate forbs and insects, whereas at Jackass Creek most of the diet was sagebrush. Larger home ranges, differences in diets, and differences in availability of forb-rich habitats possibly were related to differences in abundance and productivity between areas.

Key words: broods, Centrocercus urophasianus, *habitat, Oregon, Sage Grouse.*

Habitat factors, including resource availability, may limit Sage Grouse (*Centrocercus urophasianus*) populations through reduced recruitment of young (Klebenow 1969, Blake 1970, Wallestad 1975, Autenrieth 1981). Stand structure and food availability are characteristics most frequently associated with habitat selection by hens with broods (Klebenow 1969, Peterson 1970, Wallestad 1971, Autenrieth 1981). Dunn and Braun (1986) found that vegetative cover and extent of habitat interspersion are the most important factors influencing summer habitat use by Sage Grouse. Forbs and insects typically constitute the primary food of chicks (Klebenow and Gray 1968, Peterson 1970, Drut et al. 1994), and forb cover is often greater at sites used by broods than at random locations (Klebenow 1969, Autenrieth 1981, Dunn and Braun 1986). Shrubs, particularly sagebrush (*Artemisia* spp.), provide escape and thermal cover (Klebenow and Gray 1968) but are not a primary component of chick diets except where forbs and insects are limited in availability (Drut et al. 1994). Peterson (1970) noted decreased use of sagebrush/grassland cover types as broods mature and ascribed these changes to differential availability of succulent forbs. Martin (1970) observed that broods typically use big sagebrush (*A. tridentata*) stands during early brood-rearing and that broods <6 weeks old use areas with lower densities of sagebrush than do older broods.

Despite numerous studies of Sage Grouse summer habitat use, knowledge of habitat use and selection by Sage Grouse hens with broods is incomplete because of small sample sizes, lack of information about use and availability of cover types and habitat components within cover types used by hens with broods, failure to distinguish habitat use by hens with broods from other adults, or no provision of information regarding population status and habitat use. Information that relates population status and habitat use is critical for Oregon because the western subspecies (*C. u. phaios*), which inhabits most of the Sage Grouse range in the state, was listed as a candidate for threatened and endangered status by the Department of Interior in 1985. This listing resulted from declines in abundance caused by depressed productivity (Crawford and Lutz 1985). The objective of the study was to determine use of cover types and habitat components by Sage Grouse hens with broods during two brood-rearing periods on two study areas with different Sage Grouse population characteristics in southeastern Oregon.

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STUDY AREAS

The study was conducted at Jackass Creek, administered by the Bureau of Land Management, and Hart Mountain National Antelope Refuge, administered by the U.S. Fish and Wildlife Service. Estimates of Sage Grouse abundance since 1980 indicated approximately 2.5 birds/km^2 and 1.5 birds/km^2 at Hart Mountain and Jackass Creek, respectively (J. Lemos, Oregon Department of Fish and Wildlife, unpublished data; W. H. Pyle, U.S. Fish and Wildlife Service, unpublished data). Summer productivity counts from 1985 through 1992, the only period for which comparable data were available, averaged 1.6 and 0.9 chicks/hen ($p < .05$) at Hart Mountain and Jackass Creek, respectively.

The Jackass Creek study area, approximately 70 km southwest of Burns, Harney County, Oregon, comprises nearly 39,000 ha. Prominent shrubs are low sagebrush (*A. arbuscula*) and big sagebrush (*A. tridentata*). Western junipers (*Juniperus occidentalis*) are present on the eastern portion of the study area. Common annual and perennial forbs include mountain dandelion (*Agoseris* spp.), hawksbeard (*Crepis* spp.), lupine (*Lupinus* spp.), and phlox (*Phlox* spp.). Grasses are principally bluegrass (*Poa* spp.) and fescue (*Festuca* spp.). Annual temperature averages 10°C, and mean precipitation is 25 cm.

The Hart Mountain National Antelope Refuge study area is 100 km southwest of Jackass Creek in Lake County, Oregon, and is 89,000 ha in size. Dominant cover consists of low sagebrush, big sagebrush, and antelope bitterbrush (*Purshia tridentata*). Areas >2000 m in elevation contain curl-leaf mountain-mahogany (*Cercocarpus ledifolius*) and trembling aspen (*Populus tremuloides*). Forb and grass composition is similar to Jackass Creek. At refuge headquarters (elevation 1700 m) annual temperature averages 6°C, and mean precipitation is 29 cm. Plant nomenclature follows Hitchcock and Cronquist (1987).

METHODS

Sage Grouse hens were radio-marked in 1989–91 (Gregg et al. 1994). At the conclusion of each field season, marked hens were recaptured, radio transmitters were removed, and a sample of previously unmarked hens was equipped with radios to maintain independence of samples among years. Radios were attached with herculite ponchos (Amstrup 1980), and all hens were fitted with numbered leg bands. Locations of radio-marked hens were obtained with portable receivers and two-element, hand-held antennae.

Cover types and habitat components used for rearing broods were identified from locations of radio-marked hens with broods. Radio-marked hens with broods were located four times weekly to identify cover types used. Monitoring of broods continued until a hen lost her brood or brood integrity disintegrated (approximately 1 August each year).

We classified cover at brood sites into one of seven cover types: big sagebrush, low sagebrush, mixed sagebrush, lakebed/meadow, mountain shrub, grassland, and juniper/aspen. Cover type descriptions were based on Soil Conservation Service information (J. Kinzel, U.S. Department of Agriculture, Soil Conservation Service, unpublished data) and previous descriptions at Jackass Creek (Trainer et al. 1983, Gregg 1992).

Study area boundaries, based on locations of radio-marked hens with broods, were determined each year with the minimum convex polygon method (Mohr 1947, Odum and Kuenzler 1955). Proportions of cover types within the area used for rearing broods were determined with a dot grid system (Avery 1977).

Each brood location was marked and served as a site for habitat sampling, which was completed within 2 days after location of a brood. Percent cover of forbs, grasses, and shrubs and frequency of occurrence of ground-dwelling insects were measured at all brood locations. We established two 10-m perpendicular transects intersecting at each brood location. The position of the first transect was determined from a randomly selected compass bearing. The intercept distance (cm) of all species of shrubs along each transect was recorded to determine canopy cover (Canfield 1941). Heights of shrubs intercepted were measured from the ground to the top of the shrub canopy and placed into one of three classes: short (<40 cm), medium (40–80 cm), or tall (>80 cm). Canopy cover of shrubs was recorded separately for each height class. Percent cover of forbs was estimated from five uniformly spaced rectangular plots (20 × 50 cm) on each transect (Daubenmire 1959).

Sampling intensity was determined by constructing a species area curve with data collected from initial sampling (Pieper 1978:12). Occurrence of ground-dwelling arthropods was established from 12 pitfall traps (Morill 1975) arranged systematically along each 23-m transect, 36 at Hart Mountain and 28 at Jackass Creek, in cover types used by broods (see Drut et al. 1994). Arthropods were classified into Scarabeidae (June beetles), Tenebrionidae (darkling beetles), Formicidae (ants), and other.

Vegetative structure of habitats available to Sage Grouse broods was characterized at randomly selected locations within cover types on each study area during the brood-rearing period. Sampling of random locations, which was concurrent with measurements taken at sites used by broods, was conducted during May and June of each year. Number of random locations sampled in each cover type was based on canopy cover of sagebrush, which represented the least variable habitat component, and was determined with the "n-test" (Snedecor and Cochran 1980:210).

Home ranges for hens with broods were determined with the McPaal home range program (Stuwe and Blohowiak 1983). Home ranges were compared for two brood-rearing periods (early: hatching to 6 weeks; and late: 7 to 12 weeks after hatching) within and between study areas with chi-square analysis (Snedecor and Cochran 1980:20). Six-week intervals were based on data from Martin (1970), which indicated hens with broods changed habitat use at this time, and from Peterson (1970), which revealed differences in foods consumed by juveniles beginning approximately 6 weeks after hatching.

Within study areas, cover types used by Sage Grouse for rearing broods were compared with availability of cover types. Between study areas, cover type availability and use were compared. We arranged data in contingency tables and analyzed them with chi-square analysis; cover types with <5 brood locations were combined and analyzed collectively. If differences were detected, confidence interval testing (Neu et al. 1974, Byers et al. 1984) was used to identify cover types used selectively. Use of cover types by hens with broods of different ages was compared with chi-square to assess possible changes in habitat use associated with age of broods. Cover types used for nesting by hens that successfully hatched clutches were compared with cover types used by hens with broods during the first 6 weeks after hatching.

Habitat components measured at brood sites were compared by chi-square analysis to random sites within the same cover types for each study area to identify which vegetative components were selected. Analysis of variance was used to test among cover types and between study areas for differences in availability (random locations) and use (brood locations) of vegetative cover (Snedecor and Cochran 1980:258). The least significant difference test was used to separate means (Snedecor and Cochran 1980:272). Results were considered significant at the 95% level.

RESULTS

Most broods (13) were produced in the big sagebrush cover type, but during early brood-rearing (hatching–6 weeks), hens with broods were most frequently found (54–67% of

TABLE 1. Use and availability of cover types in which Sage Grouse broods were produced and those used for early (hatching–6 weeks) and late (7–12 weeks) brood-rearing periods at Jackass Creek and Hart Mountain, Oregon, 1989–91.

	Jackass Creek					Hart Mountain				
	Used (% frequency)			Available (% of area)		Used (% frequency)			Available (% of area)	
Cover type	Hatched ($N = 7$)	Early ($N = 7/84$)[a]	Late ($N = 3/40$)[a]	Early	Late	Hatched ($N = 11$)	Early ($N = 11/89$)[a]	Late ($N = 4/40$)[a]	Early	Late
Big sagebrush	42	17	45	54	30	91	32	52	30	57
Low sagebrush	29	53	17	32	30	9	67	38	48	16
Mixed sagebrush	29	29	20	9	15	0	0	0	1	1
Lakebed/ meadow	0	0	15	3	23	0	0	8	3	5
Other	0	0	3	2	2	0	1	2	18	21

[a] Number of broods/number of locations.

observations) in low sagebrush cover (Table 1). Three cover types were used differentially during early brood-rearing: low sagebrush was used more ($p < .05$) than expected on both areas, mixed sagebrush was used in greater proportion ($p < .05$) than available at Jackass Creek, and big sagebrush was used to a lesser extent ($p < .05$) than available at Jackass Creek. None of the other cover types was used during the early brood-rearing period.

During late brood-rearing (7–12 weeks) habitat use shifted to predominantly big sagebrush (45–52% of observations). Use of low sagebrush declined on both areas (Table 1). Availability of low sagebrush within areas used by hens with broods declined from 48 to 16% at Hart Mountain as hens with broods moved away from low-sagebrush–dominated areas. Also, during late brood-rearing, use of lakebeds and meadows increased; these habitats received the greatest use after brood break-up in August.

Forb cover ranged from 10 to 14% at sites used by hens with broods during the early brood-rearing period (Table 2) and was greater ($p < .01$) at sites used by broods than at random locations at Jackass Creek. At Hart Mountain, forb cover was used in proportion to availability during early brood-rearing (Tables 2, 3). During late brood-rearing, forbs were used in greater ($p < .01$) proportion than available at Hart Mountain, where sites used by broods had 19–27% forb cover. No use pattern in relation to forb availability was evident at Jackass Creek during late brood-rearing. There were no differences in use and availability for any shrub cover category in low ($p > .50$), big ($p > .20$), or mixed ($p > .20$) sagebrush stands. Only in lakebed/meadow habitat at Jackass Creek during the late brood-rearing period were use and availability of shrub cover different ($p = .05$). In that instance, cover of short and medium shrubs was approximately twice as great at sites used by broods as at random locations (Tables 2, 3).

Hart Mountain had more forb cover ($p < .05$) and less tall shrub cover ($p < .05$) than Jackass Creek (Table 3). In addition, there was more ($p < .05$) short shrub cover available during the early brood-rearing period at Jackass Creek than at Hart Mountain. The greatest availability of forb cover on both areas was in lakebed/meadow habitat during late-brood-rearing (14 and 21% at Jackass Creek and Hart Mountain, respectively). Hart Mountain supported greater ($p < .01$) frequencies of ground-dwelling arthropods than did Jackass Creek, but no differences were found within study areas between time periods or cover types except at Jackass Creek, where mixed sagebrush had a greater ($p = .05$) frequency of invertebrates during the early period than did low sagebrush (Table 4).

At Hart Mountain, big sagebrush and lakebed/meadow habitats supported more ($p < .05$) forbs than did low sagebrush during late brood-rearing (Table 3). At Jackass Creek low and big sagebrush supported the same cover of forbs (6%) during late brood-rearing, but the lakebed/meadow habitat had greater ($p < .05$) forb cover (14%). There was more ($p < .05$) cover of medium and tall shrubs in big sagebrush stands compared with low sagebrush (Table 3).

Mean home range sizes at Hart Mountain, were 800 and 100 ha for the early and late periods, respectively, whereas at Jackass Creek mean home ranges were 2100 and 5100 ha, respectively. Home range size was smaller ($p = .02$) in the late period than the early period at Hart Mountain, whereas home range size increased ($p < .01$) during the late period at Jackass Creek. Home range size was smaller ($p < .01$) at Hart Mountain than at Jackass Creek during both periods.

DISCUSSION

Sage Grouse hens with broods displayed similar use of cover types on the two study areas. The change in cover-type use of successfully nesting hens from big sagebrush to low sagebrush during the first 6 weeks after hatching was unique to this study. Perhaps availability of foods partially accounted for this change in use of cover types. Klebenow (1969), Peterson (1970), Wallestad (1971), Autenrieth (1981), and Dunn and Braun (1986) reported relationships between habitat use by broods and food availability. Return to use of big sagebrush during weeks 7–12 after hatching was similar to findings elsewhere. Canopy cover and shrub height at brood sites in Montana changed from 6% and a range of 15–30 cm, respectively, in June to 12% and 30–45 cm in August (Peterson 1970). Pyrah (1971) and Wallestad (1971) noted sagebrush height was greater in cover types used by broods during

TABLE 2. Vegetative characteristics of sites within cover types used by Sage Grouse hens with broods during early (hatching–6 weeks) and late (7–12 weeks) brood-rearing periods at Jackass Creek and Hart Mountain, Oregon, 1989–91.

	% cover (SD)											
	Low sagebrush				Big sagebrush				Mixed sagebrush		Lakebed/meadow	
	Jackass Creek		Hart Mountain		Jackass Creek		Hart Mountain		Jackass Creek		Jackass Creek	Hart Mountain
Vegetative class	Early (*N* = 44)	Late (*N* = 7)	Early (*N* = 60)	Late (*N* = 15)	Early (*N* = 16)	Late (*N* = 18)	Early (*N* = 27)	Late (*N* = 21)	Early (*N* = 23)	Late (*N* = 7)	Late (*N* = 6)	Late (*N* = 3)
Forb	14 (5)	3 (1)	11 (3)	19 (5)	10 (4)	9 (3)	14 (5)	19 (4)	14 (4)	12 (4)	2 (3)	27 (9)
Grass	8 (4)	3 (1)	14 (5)	17 (6)	10 (4)	11 (8)	15 (7)	16 (8)	9 (6)	9 (5)	6 (4)	1 (1)
Shrub												
Short (<40 cm)	25 (7)	36 (9)	22 (8)	19 (9)	5 (3)	5 (3)	18 (9)	17 (9)	21 (8)	13 (8)	23 (13)	0
Medium (40–80 cm)	1 (1)	0	0	0	15 (7)	14 (7)	9 (10)	14 (17)	6 (6)	12 (7)	20 (13)	0
Tall (>80 cm)	0	0	0	0	2 (4)	4 (5)	0	0	1 (1)	4 (11)	0	0

TABLE 3. Vegetative characteristics of available cover in habitats used by Sage Grouse during early (hatching–6 weeks) and late (7–12 weeks) brood-rearing periods at Jackass Creek and Hart Mountain, Oregon, 1989–91

	% cover (SD)											
	Low sagebrush				Big sagebrush				Mixed sagebrush		Lakebed/meadow	
	Jackass Creek		Hart Mountain		Jackass Creek		Hart Mountain		Jackass Creek		Jackass Creek	Hart Mountain
Vegetative class	Early (*N* = 74)	Late (*N* = 50)	Early (*N* = 80)	Late (*N* = 56)	Early (*N* = 51)	Late (*N* = 20)	Early (*N* = 72)	Late (*N* = 30)	Early (*N* = 51)	Late (*N* = 30)	Late (*N* = 25)	Late (*N* = 20)
Forb	9 (5)	6 (2)	10 (4)	8 (3)	9 (6)	6 (2)	13 (6)	14 (5)	6 (4)	3 (2)	14 (14)	21 (17)
Grass	6 (3)	6 (3)	11 (6)	12 (7)	10 (6)	8 (3)	12 (6)	13 (7)	7 (5)	6 (4)	4 (5)	1 (1)
Shrub												
Short (<40 cm)	24 (8)	28 (10)	18 (8)	21 (9)	5 (4)	8 (6)	17 (11)	17 (9)	8 (10)	21 (8)	11 (10)	0
Medium (40–80 cm)	1 (1)	0	0	0	12 (6)	13 (7)	17 (12)	16 (11)	5 (5)	9 (6)	10 (10)	0
Tall (>80 cm)	0	0	0	0	5 (6)	9 (10)	1 (2)	1 (4)	3 (7)	2 (3)	0	0

TABLE 4. Frequencies of occurrence (%) of major insect groups available during early (hatching–6 weeks) and late (7–12 weeks) Sage Grouse brood-rearing periods at Jackass Creek and Hart Mountain, Oregon, 1989–91.

	Low sagebrush				Big sagebrush			Mixed sagebrush	
	Jackass Creek		Hart Mountain		Jackass Creek	Hart Mountain		Jackass Creek	
Family	Early (*N* = 102)	Late (*N* = 84)	Early (*N* = 120)	Late (*N* = 36)	Early (*N*=12)	Early (*N* = 60)	Late (*N* = 36)	Early (*N* = 60)	Late (*N* = 60)
Scarabeidae	1	0	10	14	0	4	9	0	0
Tenebrionidae	11	8	17	14	28	16	27	15	12
Formicidae	42	47	68	62	42	81	76	61	41
Other	49	38	70	74	37	97	96	52	51

late summer; sagebrush canopy cover used by hens with broods changed from 14% in June to 21% in September (Pyrah 1971).

Cover types used by hens with broods typically had greater availability of forbs during periods of high use, but differences in availability between areas influenced use of cover types, movements, and diets. Hens at Jackass Creek selectively used sites with forb cover greater than typically found there and similar to that generally available to broods at Hart Mountain. This amount of forb cover (12–14%) may represent the minimum needed for brood habitat in Oregon. The lack of a relationship between brood use and forb availability during the late brood-rearing period at Jackass Creek likely was related to the dietary shift by chicks to sagebrush during this time (Drut et al. 1994).

Home ranges of hens with broods were larger at Jackass Creek than at Hart Mountain and increased over time. May and Poley (1969) observed no movements from meadows until fall in Colorado, and in Montana brood home ranges decreased from 85 ha in June to 51 ha in August (Wallestad 1971). The large home ranges at Jackass Creek reflected differences in forb availability and chick diets between areas (Drut et al. 1994). Chicks consumed primarily forbs and insects at Hart Mountain but ate mostly sagebrush at Jackass Creek (Drut et al. 1994). Home ranges in Idaho were larger for hens with broods than for broodless hens (406 ha and 174 ha, respectively), which possibly was related to forb use (Connelly and Markham 1983). These authors also noted that Sage Grouse may occupy larger summer home ranges in wet years because of greater availability of forbs. Differences in availability of brood-rearing habitats, dietary intake of chicks, and home range sizes perhaps are related to differences in productivity and abundance of Sage Grouse at the two study areas.

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NEEDLE BIOMASS EQUATIONS FOR SINGLELEAF PINYON ON THE VIRGINIA RANGE, NEVADA

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ABSTRACT.—Foliar biomass of singleleaf pinyon (*Pinus monophylla* Torr. & Frem.) was estimated on the Virginia Mountains, Nevada, based on the easily measured dimensions of crown volume and sapwood area. Leaf biomass estimation techniques used in other studies of pinyon where total leaf biomass was collected were supported. Both sapwood area (cm^2) and crown volume, calculated as one-half of an ellipsoid (m^3), were found to be significantly related to total dry weight needle mass (g). Best predictive equations for crown volume were obtained with nonlinear regression analysis. A previously reported two-part relationship based on tree size for predicting needle biomass with sapwood area was supported. Foliar biomass of singleleaf pinyon can be accurately estimated with a minimum of 10 sapwood cores.

Key words: singleleaf pinyon, foliage biomass, sapwood area, biomass prediction.

In recent years land managers trying to fulfill the goal of multiple use have needed to ascertain the potential value and use of pinyon-juniper woodlands extending over 17 million ha across the Rocky Mountain and Great Basin regions (Chojnacky 1986). Singleleaf pinyon and Utah juniper (*Juniperus osteosperma* Little) woodlands cover more than 6 million ha in the Great Basin alone (Tausch and Tueller 1990). This forest type has historically supplied fuelwood, charcoal, nuts, fence posts, and poles (Fogg 1966), especially during heightened mining activity in the late 1800s (Budy and Young 1979). Pinyon-juniper forests also provide essential areas for wildlife habitat (McCulloch 1969, Short and McCulloch 1977, Balda and Masters 1980). Balancing out these benefits is the nearly complete loss of forage and potential increased soil erosion resulting from the establishment of this species (Doughty 1987).

Estimates of biomass are essential to most studies of plant community competition, succession, and resource allocation including studies of pinyon-juniper woodlands. Total foliar biomass, or phytomass, can be vital to assessment of plant water-use efficiency (Long et al. 1981, Waring 1983), nutrient cycling (Waring and Running 1978), soil moisture conditions (Grier and Running 1977), the hydrologic environment (Nemani and Running 1989), and competitive interactions (Tausch and Tueller 1990). The amount of foliage biomass on a tree is strongly related to the area of conducting tissue transporting water and nutrients to these tissues. This relationship has been found for many conifers (Grier and Waring 1974, Kaufmann and Troendle 1981, Marchand 1984, Miller et al. 1987), including pinyon (Tausch and Tueller 1989). Survival of trees in arid environments demands efficiency, and production of excess xylem and associated supporting tissue would waste precious resources. Alternately, insufficient development of conducting tissue would dehydrate and starve a tree. Also, as a tree grows, its mass and the spatial volume it inhabits expand in a nonlinear fashion (Tausch and Tueller 1988).

Many studies have shown close relationships between whole-tree phytomass and easily measured plant dimensions (Budy et al. 1979, Miller et al. 1981, Cochran 1982, Hatchell et al. 1985, Tausch and Tueller 1989, 1990). Measuring needle mass of entire singleleaf pinyon (*Pinus monophylla* Torr. & Frem.) trees through harvest can be inefficient and expensive (Meeuwig and Budy 1979), especially on large trees in remote areas. The ability to accurately estimate phytomass based on simple allometric measurements can greatly ease the process. Cross-sectional sapwood areas for pinyon pine can be estimated with a high degree of accuracy using increment cores and trunk diameter measurements (Whitehead 1978, Tausch 1980). Equations generated by these procedures can apparently vary for this

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species depending on location in the Great Basin (Tausch and Tueller 1988). Development and refinement of techniques to acquire reliable mensurational data will only enhance the further study, understanding, and proper management of pinyon-juniper woodlands. The objective of this study was to apply evolved methods of estimating whole-tree needle biomass to singleleaf pinyon on a third Great Basin site.

METHODS

Study Area

Research was conducted on USDI Bureau of Land Management pinyon-juniper woodlands 32 km SE of Reno, Nevada (39°17'30"N, 119°42'30"W). The study site lies at 1963 m elevation in a near level east-west saddle formed between a basalt plug and the west-facing slope of the Virginia Mountains. Soils are 0–10 cm deep and poorly developed from decomposed Cretaceous granodiorite and Pliocene-Pleistocene volcanics. This area receives approximately 336 mm of precipitation annually (Desert Research Institute 1991), mostly as snow. Some Utah juniper occurs in the area, but singleleaf pinyon is the dominant tree species.

Field Techniques

Tree selection procedures were based on the five maturity classes described in Blackburn and Tueller (1970). Ten trees from each maturity class were randomly selected for potential measurement within relationships of accessibility associated with placing potometers for tree water-use studies (De Rocher 1992). Five trees from each maturity class were randomly selected for a total of 25 trees to be measured and harvested. Total tree height (cm), canopy height (cm), maximum canopy diameter and canopy diameter perpendicular to the maximum (cm), and trunk circumference (cm) at approximately 15 cm above the root crown were determined for all trees.

Past studies have shown that including estimates of canopy density improves predictability of needle biomass (Miller et al. 1981), but visual estimates used were not easily comparable between studies. Canopy needle biomass density decreases as voids develop within the canopy with increasing age. Error can be introduced in needle biomass estimation based on crown volume calculated from simple canopy dimensions without an estimate of the voided space. This study incorporated a grid method of determining average canopy density similar to the method proposed by Belanger and Anderson (1989). The procedure involved viewing each sampled tree canopy through a 6 × 60-cm Plexiglas sheet that had a 3-cm^2 grid transposed onto it. A perspective was chosen that approximated an average of canopy fullness that was sufficiently distant to visually contain the entire tree height within the vertically held grid when viewed at arm's length. First, the left upright edge of the grid was then aligned with the trunk and the canopy height centered within the grid. This placed the grid over the right side of the tree. Within the grid a smooth canopy border was imagined as if a ribbon were stretched from the top along the outside edge of the canopy to the base. Next, grid squares more than halfway within this perimeter line were counted for the maximum area covered by the canopy. Last, squares within the perimeter covered by >50% foliage (versus open space, trunk, or branches) were counted. Dividing the number of foliage-covered squares by the total number of squares within the canopy perimeter determined a ratio of relative canopy density. This procedure was then repeated by placing the grid over the left side of the tree canopy.

Following crown measurements and estimation of canopy density, all green foliage was harvested by cutting off branches and placing them in feed bags. After being air-dried, the needles were dried at 80°C for 24 h to achieve consistency and then weighed. A trunk cross section was also cut approximately 15 cm above the root crown. These cross sections were measured for sapwood area (cm^2) using a paper trace, which was cut into small pieces and run through a model LI-3100 leaf area meter (LI-COR, Inc., Lincoln, Nebraska).

Analysis Techniques

Longest crown diameter, diameter perpendicular to it, and crown height for each tree were used to compute the crown volume (m^3) based on the formula for one-half of an ellipsoid (Tausch 1980, Beyer 1984). Crown volume was also adjusted for canopy density by

TABLE 1. Singleleaf pinyon foliar mass prediction models using sapwood area and crown volume approximated as one-half of an ellipse.

Relation	Equation	R^2	Standard error of estimate
	Linear regression		
Needle vs. sapwood Mass (g) Area (cm^2) (All maturity classes)	$Y = 265.3 + 122.1X$	.977	4059
Needle vs. sapwood Mass (g) Area (cm^2) (Trees <40cm^2 sapwood)	$Y = -142.5 + 106.4X$	.947	227
Needle vs. sapwood Mass (g) Area (cm^2) (Trees >40cm^2 sapwood)	$Y = 3234.7 + 117.4X$	.971	6822
	Log transformed linear regression		
Needle vs. sapwood Mass (g) Area (cm^2) (All maturity classes)	$\ln Y = 35.31 + 1.24 \ln X$	.782	16,886
Needle vs. sapwood Mass (g) Area (cm^2) (Trees <40cm^2 sapwood)	$\ln y = 33.9 + 1.37 \ln X$	.973	194
Needle vs. sapwood Mass (g) Area (cm^2) (Trees >40cm^2 sapwood)	$\ln Y = 186.5 + 0.94 \ln X$	.970	6453
	Nonlinear regression		
Needle vs. sapwood Mass (g) Area (cm^2) (All maturity classes)	$Y = 181.4X^{0.94}$	.989	3847
Needle vs. sapwood Mass (g) Area (cm^2) (Trees <40cm^2 sapwood)	$Y = 20.1X^{1.497}$	.995	83
Needle vs. sapwood Mass (g) Area (cm^2) (Trees >40cm^2 sapwood)	$Y = 194.4X^{0.929}$	.970	6444
Needle vs. ellipsoid Mass (g) Volume (m^3) (All maturity classes)	$Y = 2.34X^{0.58}$	.976	5643
Needle vs. ellipsoid Mass (g) Volume (m^3) (Adjusted for canopy density) (All maturity classes)	$Y = 1.36X^{0.62}$	.977	5459

multiplying the calculated volume by the canopy density ratio. Two types of regression analyses were used to evaluate relationships between oven-dry foliage weight and sapwood area and crown volume. Prediction equations utilizing any form of data transformation to linearize the data for least-squares analysis were repeated using nonlinear regression with the original untransformed data (Tausch and Tueller 1988), and the best fit results are reported. Comparisons among regression results were made using highest coefficients of determination (R^2) and lowest standard error of the estimate values, to a level of significance of $p < .01$ for the least-squares analyses results.

RESULTS AND DISCUSSION

The amount of foliage supported per unit area of conducting tissue ranged from 37.4 g cm^{-2} for the smallest tree to 157.2 g cm^{-2} for one of the largest, and averaged 88.8 g cm^{-2} for all sampled trees. Using a nonlinear regression technique that iteratively approximates optimal fit without data transformation provided as tight a fit to the full data set as linear regression utilizing log-transformed data in relating dried needle mass and sapwood area. Reapplication of untransformed data to linear models decreased the relationship (Table 1). For trees with <40 cm^2 sapwood area (maturity classes 1–3), this relationship was definitely nonlinear, as was observed by Tausch and Tueller (1989). The slope of the linear regression line for these western Nevada data is nearly identical to the slope for pinyon from southwestern Utah (Tausch 1980), suggesting a potential singular relationship across the Great Basin. For both these data and the Tausch 1980 southwestern Utah data, the entire foliage was harvested from each tree. A similar relationship was not found between data from Tausch 1980 and Tausch and Tueller 1989. Tausch and Tueller (1989) utilized a foliage subsampling technique to estimate total needle biomass, which may have underestimated the needle biomass to sapwood area ratio.

Correlation between needle biomass and the calculated elliptical crown volume was also significant by nonlinear regression (Table 1). When adjusted for percent canopy density, the linear elliptical volume relationship was improved (R^2 = .98), and the standard error of the estimate simultaneously was reduced from 5643.1 to 5458.9.

CONCLUSIONS

Prediction of foliar mass using sapwood area of singleleaf pinyon on the Virginia Mountains, Nevada, was equivalent in precision to previously reported results for this species conducted in southwestern Utah (Tausch 1980). Elliptical crown volume calculated from canopy widths and crown height again proved to be a significant predictor of dry weight phytomass. Adding an estimate for variations in canopy density further improved the relationships. As previously reported (Tausch and Tueller 1989), application of nonlinear regression analysis produced the best fit between phytomass and all tree dimensions, as reflected by increased coefficient of determination values and reduced standard errors of the estimate over other regression methods.

Estimates of singleleaf pinyon phytomass for hydrological and ecological studies of pinyon-juniper woodlands can be most accurately obtained from a minimum of 10 sapwood area measurements. Canopy dimensions and an assessment of foliage density can also be used to reliably estimate whole-tree phytomass. This study, conducted on the western edge of the Great Basin, achieved needle biomass regressions based on sapwood area that were nearly identical to those from work performed in southwestern Utah. Future research should concentrate on comparing numerous isolated studies across the Great Basin of whole-tree foliar mass harvest so that a regional biomass equation may be developed.

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SOME PHYSIOLOGICAL VARIATIONS OF *AGROPYRON SMITHII* RYDB. (WESTERN WHEATGRASS) AT DIFFERENT SALINITY LEVELS

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Abstract.—The purpose of this study was to determine the physiological responses of *Agropyron smithii* Rydb. to various saline environments as evaluated in the laboratory. *Agropyron smithii* Rydb. (Rosana) seeds were germinated, transplanted into nutrient solutions with NaCl concentrations of 0, 50, 100, 150, and 200 m*M*, and grown for 80 days in a growth chamber. Results indicated that leaf water potential, relative water content of leaf tissue, and concentrations of Na, K, and Cl in plant tissue were significantly affected by increasing NaCl concentration. However, leaf chlorophyll concentration and concentrations of Ca and Mg in plant tissue were not significantly affected by the presence of NaCl.

Key words: Agropyron smithii, *salinity, physiology, chlorophyll, sodium, potassium, calcium, magnesium, water potential, chloride.*

Agropyron smithii Rydb. (western wheatgrass) is a strongly rhizomatous, glaucous, often glabrous, long-lived perennial grass. It is palatable, cures well on the ground, and is a native grass of the northern Great Plains (Judd 1962, Schultz and Kinch 1976, Stubbendieck et al. 1986). Because *A. smithii* is a valuable grazing species in the arid West, it is often sought out for revegetation of these soils.

Research has shown that salt stress has an impact on chlorophyll concentrations of leaves, leaf osmotic potentials, and mineral uptake and transport in many plants. Seemann and Critchley (1985) reported that chlorphyll concentration per unit area of *Phaseolus vulgaris* L. was reduced considerably by NaCl stress. Macler (1988) also reported that in *Gelidium coulteri* (red alga) the content of chlorphyll was altered with a change in NaCl concentration in the growth media. However, Antlfinger (1981) found that concentrations of chlorophyll *a*, chlorophyll *b*, and total chlorophyll of *Borrichia frutescens* were not significantly influenced by salinity.

Clipson et al. (1985) used a dew-point hydrometer to measure leaf osmotic potential of *Suaeda maritima* L. Dum. seedlings grown under different salinities. They found that leaf osmotic potentials were lower (more negative) for those grown under higher salt concentrations. Black (1960) reported that, under saline conditions, the osmotic potential of *Atriplex vesicaria* leaves changed in the direction that maintained a constant water potential gradient between leaf and soil.

Evidence is growing that salt stress inhibits the uptake and transport of mineral nutrients in some plants. In *Hordeum vulgare* L. (barley) seedlings, the uptake and transport of nitrogen (Aslam et al. 1984), phosphate (Maas et al. 1979), K (Lynch and Läuchli 1984), and Ca (Lynch and Läuchli 1985) were reduced by salinity. The transport of K and Ca in *Gossypium hirsutum* L. was also disrupted by high Na^+ concentrations (Cramer et al. 1987). In *Salicornea europa* the uptake of K^+, Mg^{2+}, and Ca^{2+} was also reduced by Na^+ (Austenfeld 1974).

A study of the physiological responses of *A. smithii* in saline environments may determine how this species adapts to saline soils and provide additional information for breeding salt-tolerant species. The purpose of this study was to measure leaf chlorophyll concentration, leaf water potential, relative water content of leaf tissue, and mineral content of *A. smithii* grown under different saline water culture conditions.

Materials and Methods

Agropyron smithii Rydb. seeds (Rosana) were germinated in moist vermiculite (temperature alternated between 15°C for 20 h

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and 30°C for 4 h) in complete darkness for 5 days. Thereafter, the seeds were held in darkness (15°C for 3 days), then at an alternating temperature (28 ± 2°C for a 12-h day and 15°C for the 12-h night) as recommended by Toole (1976).

A nutrient solution modified from Arnon and Hoagland (1940) was used in this study (Table 1). One-liter plastic containers were used to hold the experimental plants and nutrient solutions. Plants were supported in square cardboard covers impregnated with paraffin. Both covers and containers were sterilized with a 5% Clorox solution before use.

When *A. smithii* seedlings were 15 days old (2–3 cm long), they were placed through holes in the cover and held in place with loose wads of cotton wrapped around each stem. Four plants were placed in each container. Each container was aerated for 30 min each 24-h period. For the first 9 days after transplanting, damaged or infected seedlings were replaced with fresh ones.

Salinization of the medium began 9 days after seedlings had been transferred to the nutrient solution. This was done by increasing NaCl concentration in the culture solutions at the rate of 25 m*M* every 4 days to the final concentrations of 50, 100, 150, and 200 m*M*. Plants grown in unsalted cultures were used as controls. The nutrient solution was changed every 12 days during the experiment.

Experiments were carried out in a Sherer Gillette Plant Growth Chamber (Model 512 CEL) set for a 12-h day at 28 ± 2°C with a humidity of 40 ± 5% and a 12-h night at 15°C with a humidity of 60 ± 5%. Light was supplied by 12 cool white VHO fluorescent bulbs. Eighty plants (20 containers) were used for each treatment, and all plants in each treatment were numbered. From these 80 plants, 10 were randomly selected for measuring for each treatment. If a plant had more than one culm, the longest was chosen for the data measurement of leaf chlorophyll, leaf water potential, and relative water content of leaf tissue.

Leaf chlorophyll concentration was determined by extracting the chlorophyll in acetone (80% v/v in water) from the second and third leaves collected from a randomly selected plant when the plants were 93 days old. Absorbance of chlorophyll was measured at 645 and 663 nm following the procedure of Witham et al. (1986).

TABLE 1. Composition of the nutrient solution modified from Arnon and Hoagland (1940).

Salt	g/L
KNO_3	1.02
$Ca(NO_3)_2 \cdot 4\,H_2O$	0.71
$NH_4H_2PO_4$	0.23
$MgSO_4$	0.24
Salt	**mg/L**
H_3BO_3	2.86
$MnCl_2 \cdot 4\,H_2O$	1.81
$CuSO_4 \cdot 5\,H_2O$	0.08
$ZnSO_4 \cdot 7\,H_2O$	0.22
$H_2MoO_4 \cdot H_2O$	0.09
$FeSO_4 \cdot 7\,H_2O$ 5 g/L & tartaric acid 4 g/L	0.6 m*L*/L (every 4 days)

Leaf water potential was evaluated by Chardokov's procedure as described by Witham et al. (1986) when the plants were 89 days old. All leaves collected from a randomly chosen plant were cut into pieces, mixed, and then equally divided into 17 test tubes containing sucrose solutions with concentrations ranging from 0.1 *M* to 0.5 *M* with increments of 0.025 molarity. The relationship between sucrose concentration and leaf water potential is shown in Witham et al. (1986).

Relative water content (RWC) of leaf tissue was determined by using the following relationship modified from Vassey and Sharkey (1989) when the plants were 84 days old:

$\% \text{ RWC} = \{(\text{FW} - \text{DW})/(\text{SAT} - \text{DW})\} \times 100$ where:

FW = leaf fresh weight in grams,

DW = oven-dried (at 105°C for 72 h) weight in grams, and

SAT = weight (in grams) of the tissue after soaking in water for 3 h.

All leaf tissue from a randomly selected plant was used for determining relative water content (RWC).

Plants selected for mineral analysis (K, Na, Ca, Mg, and Cl) were harvested when they were 80 days old. Ten randomly selected plants were washed with distilled water and then placed in an oven at 105°C for 72 h. Dry material from each plant was weighed, ground, and then transferred into a crucible that was ashed in a muffle furnace at 500°C for 4.5 h. The ash was dissolved in 20% HNO_3 and filtered for the determination of K, Na, Ca, and Mg concentrations. Concentrations of K and Na were determined with a flame emission spectrophotometer (Perkin-Elmer, Model 403), and concentrations of Ca, and Mg were determined with an atomic absorption spectrophotometer (also Perkin-Elmer, Model 403).

The Cl concentration was determined indirectly by adding a known excess of silver to the sample solutions, which resulted in precipitation of the Cl as AgCl (Perkin-Elmer Corporation 1971). After the separation of AgCl, the concentration of unreacted silver was determined by atomic absorption. Concentrations of Cl were calculated using the formula listed at the end of this paragraph. Samples were prepared by placing the oven-dried plants in a muffle furnace at 500°C for 10 h. The ash was dissolved in distilled water (24–67 m*L*) to obtain a solution with a Cl concentration of 0–1000 μg/m*L* Cl and then filtered. Ten m*L* of sample, 2 m*L* of concentrated nitric acid, and 10 m*L* of silver nitrate solution (5000 μg/m*L* Ag) were transferred into a volumetric flask and diluted with distilled water to a volume of 100 m*L*. Thirty (30) m*L* of the mixed solution was centrifuged for 10 min at 2500 rpm. The supernatant was diluted with water 1:100 (v/v). Concentrations of Ag in the diluted supernatant were measured by atomic absorption (Perkin-Elmer, Model 403). Concentrations of Cl^- in the samples were calculated as follows (Perkin-Elmer Corporation 1971):

Chloride (mg/m*L*) = {500 – 100 × (mg/m*L* Ag in supernatant)} × 3.29 × DF where:

DF = dilution factor(s).

One-factor ANOVA, following procedures outlined by Kleinbaum et al. (1988), was used to determine statistically significant differences ($\alpha = .05$) among treatments.

RESULTS

Leaf water potential, relative water content of leaf tissue (RWC), and concentrations of Na, K, and Cl in plant tissue were significantly affected by the presence of NaCl, whereas concentrations of leaf chlorophyll, Ca, and Mg in the plant tissue were not (Table 2).

Mean values of leaf water potential decreased (were more negative) as external NaCl concentrations increased. The range was –0.34 MPa to –0.96 MPa for plants grown in nutrient solutions with 0 m*M* and 200 m*M* NaCl, respectively. RWC decreased as NaCl concentration in nutrient solutions increased and varied from a maximum of 88% to a minimum of 79% for the plants grown in solutions with 0 m*M* and 200 m*M* NaCl, respectively (Table 2).

Concentrations of Na, Cl, K, and Ca in *A. smithii* tissue increased with an increase in NaCl concentration. Mean values ($n = 10$) of Na concentration varied from a minimum of 1.6 mg/g to a maximum of 58 mg/g (dry weight) for plants grown in solutions with 0 m*M* and 200 m*M* NaCl, respectively (Table 2).

Plant Cl concentration increased from 2.7 mg/g to 35 mg/g (dry weight) for plants grown in solutions with 0 m*M* NaCl and 200 m*M* NaCl, respectively. Potassium concentration increased from 47 mg/g to 59 mg/g (dry weight). Calcium concentration varied from a minimum of 4.5 mg/g to a maximum of 5.1 mg/g (dry weight). No appreciable change in Mg concentrations was observed, although they decreased from a maximum of 2.7 in control plants to 2.4 mg/g (dry weight) in plants grown in solutions with 200 m*M* NaCl (Table 2).

DISCUSSION

Concentrations of chlorophyll *a*, chlorophyll *b*, and total chlorophyll in leaf tissue were not significantly affected by NaCl treatments (Table 2). This finding agrees with the previous study of *Borrichia frutescens* by Antlfinger (1981) but not with the study of Seemann and Critchley (1985) on *Phaseolus vulgaris* L. This discrepancy might be a result of using different methods of expressing chlorophyll concentrations. The unit used in this study was mg chlorophyll/g fresh tissue, while the unit used by Seemann and Critchley (1985) was g chlorophyll/m^2 leaf area. Since water content of *A. smithii* leaves decreased significantly as salinity increased (Table 2), this might have caused the values of chlorophyll concentration to be overestimated for plants grown in solutions with high concentrations of NaCl because of reduction of leaf fresh weight. If chlorophyll concentrations of *A. smithii* were expressed as g/unit leaf area, the treatment difference might have been apparent. Further study is needed to confirm this thesis.

TABLE 2. Leaf chlorophyll content (mg/g fresh tissue), leaf water potential (MPa, 20°C), relative water content of leaf tissue (RWC %), and mineral content of a whole plant (mg/g in dry weight) of *A. smithii* grown in nutrient solutions with five NaCl concentrations. Values represent mean (n = 10) ± 1 SD. Significance of the F-test from the ANOVA is also given.

	Treatments (m*M* NaCl)					
Character	0	50	100	150	200	Significance level
Chlorophyll *a*	1.3 ± 0.24	1.5 ± 0.19	1.4 ± 0.23	1.4 ± 0.21	1.4 ± 0.24	.2289
Chlorophyll *b*	0.9 ± 0.16	1.0 ± 0.17	1.0 ± 0.15	0.9 ± 0.14	0.9 ± 0.20	.2919
Total chlorophyll	2.2 ± 0.39	2.6 ± 0.35	2.4 ± 0.36	2.4 ± 0.34	2.3 ± 0.42	.2166
Leaf water potential	−0.34 ± 0.06	−0.6 ± 0.1	−0.8 ± 0.07	−0.89 ± 0.07	−0.96 ± 0.07	.0001
RWC	88 ± 3.8	87 ± 1.3	83 ± 6.9	81 ± 7.2	79 ± 3.6	.0003
Sodium[a]	1.6 ± 0.15	37 ± 4.8	48 ± 4.9	54 ± 5.2	58 ± 5.4	.0001
Chloride[a]	2.7 ± 0.25	7.3 ± 0.76	18 ± 1.4	30 ± 2.4	35 ± 2.7	.0001
Potassium	47 ± 4.4	55 ± 5.3	57 ± 5.8	58 ± 5.8	59 ± 5.6	.0001
Calcium	4.5 ± 0.51	4.9 ± 0.64	4.9 ± 0.64	5 ± 0.64	5.1 ± 0.7	.2803
Magnesium	2.7 ± 0.21	2.6 ± 0.43	2.4 ± 0.35	2.5 ± 0.23	2.4 ± 0.26	.4421

[a] Test of significance was performed on the transformed data (common logarithms).

Several environmental factors that influence chlorophyll content in *A. smithii* have been identified. Lauenroth and Dodd (1981) discovered that when *A. smithii* was exposed to SO_2, chlorophyll *a* and *b* concentrations were reduced. Chlorophyll *a* was found to be more sensitive to SO_2 than was chlorophyll *b*. Bokhari (1976) found that temperature, water stress, and nitrogen fertilizer also influenced the content of chlorophyll *a* and *b*.

There was a significant change in leaf water potential of *A. smithii* along the salinity gradient. Leaf water potential became lower (more negative) in response to increased levels of NaCl (Table 2). The decline of leaf water potential caused by salinity has also been found in other plants such as *Cochleria officinalis, Atriplex littoralis,* and *Limonium vulgare* (Stewart and Ahmad 1983).

Reduction of tissue water potential induced by the addition of salt into the nutrient solution has several impacts on plants that are similar to those induced by water stress. Examples of these are the inhibition of cell growth, cell wall synthesis, protein synthesis, carbon assimilation, respiration (Glass 1988), photosynthesis (Black and Bliss 1980), and other enzyme activities (Stewart and Ahmad 1983).

Reduction of leaf water potential was thought to be a strategy to maintain turgor and avoid desiccation in saline environments (Glass 1988). The change of leaf water potential can occur in a variety of ways, such as changing osmotic potential or turgor pressure, or the combination of the two. However, studies of angiosperm halophytes by Stewart and Ahmad (1983) have shown that changes in cell osmotic potential are the major components that effect changes in leaf water potential. In leaf tissue of *Limonium vulgare*, leaf water potential and osmotic potential decreased in a parallel fashion over a change in growth media water potential from near zero to −2.7 MPa. The turgor potential was more or less constant up to −1.8 MPa. When *L. vulgare* was grown in media having salinity greater than −2.7 MPa, turgor pressure often decreased. It is currently believed that the decrease in turgor pressure is the primary event inhibiting growth. Plant cells will grow only when the protoplast exerts a positive pressure on the cell wall. Crop plants were found severely wilted when leaf water potentials were lower than a range of −1.2 to −1.6 MPa (Hanson et al. 1977). Thus, the ability of plants to maintain their leaf water potentials above the turgor loss point in a saline environment may be used as a measure of their salt tolerance. Data from the present study are unable to predict (1) the value of leaf water potential at which *A. smithii* will lose its turgor or (2) how osmotic potential and turgor pressure respond to water stress induced by saline environment.

RWC of leaf tissue is sometimes used to indicate the degree of water deficit. This value in *A. smithii* was significantly reduced by the presence of NaCl in nutrient solutions (Table 2). Although RWC has a positive relationship with tissue turgor pressure, the correlation between these two parameters varies from species to species. For example, at the same value of RWC, *Dubautia ciliolata* is able to maintain a higher value of turgor pressure than *D. scabra* (Robichaux 1984). The ability to maintain higher turgor pressure is thought to be an adaptation to water stress induced by salt. Further study is needed to explore the relationships of RWC, osmotic potential, and turgor pressure of *A. smithii* in saline environments.

The concentration of Na ion in *A. smithii* increased dramatically as the external NaCl increased (Table 2). An increase in Na ion has also been found in leaf tissue of *Phaseolus vulgaris* L. grown in saline environments (Seemann and Critchley 1985). The accumulation of high concentrations of Na ion was thought to balance the low water potential of the external environment in halophytes (Glass 1988). Data from this study suggest that *A. smithii* may use the same method as other halophytes to maintain a more negative osmotic potential than that of the external medium.

Accumulation of Na in *A. smithii* tissue also accounts for the reduced growth of this plant, because enzymes of all eukaryotes are sensitive to high concentrations of NaCl (Kramer 1984) and high concentrations of Na cause a disruption of membrane integrity by displacement of Ca from cell surfaces by Na (Cramer et al. 1985, Lynch and Läuchli 1988). Moreover, Cramer et al. (1987) and Jeschke (1984) suggested that a high level of Na in the apoplast could also inhibit the transport of assimilate and K in the phloem, thus reducing growth.

For most plants to survive in saline environments, Na must be excluded from the bulk cytoplasm. In halophytes it has been demonstrated that Na concentrations are relatively low in the cytoplasm compared to the vacuole. In the root cortical cells of the halophyte *Suaeda maritima* (L.) Dum., Na was found in the vacuoles at four times the concentration in the cytoplasm or cell walls (Hajibagheri and Flowers 1989). Jeschke (1980) suggests that this kind of Na compartmentalization appears to be brought about by selective K ion influx and Na efflux through the plasmalemma and by Na^+/K^+ exchange across the tonoplast.

In addition to cellular Na compartmentalization, plants employ other methods to avoid or minimize toxic effects of Na. For example, *Distichlis stricta* (Torr.) Rydb., *Atriplex halimus* L. (Mozafar and Goodin 1970, Anderson 1974), and members of the families *Plumbaginaceae* and *Frankeniaceae* (Helder 1956) have salt-eliminating glands or hairs that are found on the leaves. In *Oryza sativa* (rice) the salt is translocated to older leaves that then drop from the plant (Yeo and Flowers 1982). Further study is needed to clarify how *A. smithii* avoids or minimizes toxic effects of salts.

Sodium is not an essential element for *A. smithii* but is now considered an essential nutrient for plants capable of fixing CO_2 via C_4 organic acids. This includes C_4 and CAM plants (Glass 1988). It is interesting to note that the C_4 plants *Zea mays* (corn) and *Saccharum officinarum* L. (sugar cane) have not been shown to require Na (Hewitt 1983).

The concentration of Cl in *A. smithii* increased considerably as the external NaCl concentration increased. But overall concentrations of Cl in *A. smithii* tissue are lower than those of Na (Table 2). The reason that *A. smithii* keeps Na concentrations higher than those of Cl in saline environments is unclear. A similar increase in Cl was found in leaf tissue of *Phaseolus vulgaris* L. grown in saline environments (Seemann and Critchley 1985). The accumulation of this element in halophyte tissue is also thought to influence osmotic regulation. Cellular Cl compartmentalization, like that of Na, has been found in *Suaeda maritima* (L.) Dum. (Hajibagheri and Flowers 1989).

Chloride basically has the same toxic effects on plants as Na does. In fact some toxic effects of NaCl may result from a combination of the two ions. In citrus and grapes, Cl has been shown to be the damaging ion (Shannon 1984). Levitt (1980) claimed that Cl injury occurred earlier and was more severe than Na injury because Cl was accumulated by plants from NaCl more rapidly than Na was. Since the accumulation of Na and Cl in plant tissue is a common phenomenon found in halophytes, the accumulation of these two ions in *A. smithii* in this study could indicate this species has some level of adaptation to saline environments.

The concentration of K ion increased in *A. smithii* as the external NaCl increased. However, the increment was not as great as that of Na and Cl (Table 2). These results are comparable to those found by Antlfinger (1981) in *Borrichia frutescens* but do not agree with the findings in *Gossypium hirsutum* L. In *G. hir-*

sutum L., the transport of potassium was disrupted by high Na^+ concentrations (Cramer et al. 1987). The discrepancy in potassium content might be because *G. hirsutum* L. is more sensitive to NaCl than are *A. smithii* and *Borrichia frutescens*. The increase of the potassium ion content of *A. smithii* in this study could be due to an altering of the ionic charges within cells resulting from the rise of Cl concentrations. Potassium is known to generate turgor in many non-halophytes and halophytes. It is also an enzyme activator with at least 60 enzymes known to be activated by this ion (Glass 1988).

Studies of cell cultures of *Nicotiana tabacum* (Watad et al. 1983), *Medicago sativa* (Croughan et al. 1979), and *Citrus aurantium* (Ben-Hayyim et al. 1985) found that a higher level of internal potassium ion could be correlated with a higher level of salt tolerance. Since *A. smithii* is able to maintain a high internal potassium ion concentration when grown in saline environments, this may be a sign of salt tolerance.

The concentration of Ca was not significantly changed by increased external NaCl concentrations (Table 2). This finding does not agree with the studies on *Hordeum vulgare* L. (barley) seedlings by Lynch and Läuchli (1985) and on *Salicornea europa* by Austenfeld (1974). The discrepancy in the findings may be due to the possibility that *A. smithii* is more tolerant to NaCl than *Hordeum vulgare* L. and *Salicornea europa*.

In *Zea mays* root protoplast, Ca is known to be displaced from associated cell membranes by high concentrations of internal Na. This displacement is correlated with increased leakage of potassium ion (Lynch and Läuchli 1988) because Ca is known to maintain cell membrane integrity for plants in saline environments (Poovaiah and Leopold 1976, Leopold and Willing 1984, Cramer et al. 1987).

Magnesium concentration did not change appreciably with increasing external NaCl concentrations (Table 2). The findings do not agree with those studies on *Salicornea europa* conducted by Austenfeld (1974). Magnesium is well known for its participation in the chlorophyll molecule. The unaltered concentration of Mg is consistent with the unaltered concentration of chlorophyll in this study. The role of this element in plants responding to external NaCl is not clear at this point.

CONCLUSIONS

The unchanged chlorophyll concentration, reduction of leaf water potential, and accumulation of K and Na of *A. smithii* in this study are signs of adaptation to saline environments. The biomass study of this species (data are not presented in this article) indicates that *Agropyron smithii* prefers an environment with a low concentration of NaCl, although it can survive in a habitat with a higher concentration of salt.

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PREVALENCE OF ECTOPARASITE INFESTATION IN NEONATE YARROW'S SPINY LIZARDS, *SCELOPORUS JARROVII* (PHRYNOSOMATIDAE), FROM ARIZONA

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Key words: chigger, Eutrombicula lipovskyana, *mite,* Geckobiella texana, Sceloporus jarrovii, *Phrynosomatidae, neonate, prevalence, intensity.*

While it is well known that ectoparasites infest lizards (Frank 1981), we know of no reports concerning how quickly newborn (neonate) lizards are infested under natural conditions. Ectoparasites have been shown to cause a diffuse inflammatory response in the skin of infected lizards from natural populations (Goldberg and Bursey 1991, Goldberg and Holshuh 1992). The purpose of this investigation is to report the age at which ectoparasite (chigger and mite) infestation first occurs in neonate Yarrow's spiny lizards (*Sceloporus jarrovii*). This lizard is well suited for determining age at which infestation first occurs since it is a live-bearing lizard in which parturition occurs within a short period of time near the end of June each year (Goldberg 1971). This contrasts with egg-laying lizards that may contain eggs for several months (Goldberg 1973), with hatchlings emerging over an extended period. Goldberg and Bursey (1992) reported on prevalence of the nematode *Spauligodon giganticus* in neonate *S. jarrovii.*

METHODS

Thirty-six neonate *S. jarrovii* were collected by hand or hand-held noose 28–30 June 1991 at Kitt Peak (31°95′N, 111°59′W, elevation 1889 m) in the Baboquivari Mountains, 85 km SW of Tucson, Pima County, Arizona. Lizards were measured to the nearest mm snout-vent length (SVL), and ectoparasites were counted at time of capture. Sizes of these wild-caught specimens were compared to 223 *S. jarrovii* neonates born of 37 female captive lizards in 1967–69 (Goldberg 1970). Specimens were deposited in the herpetology collection of the Los Angeles County Natural History Museum (LACM) (139070–139105).

RESULTS AND DISCUSSION

Lizards in the 1991 sample averaged 30.1 ± 2.0 mm SVL, range 26–36 mm. Eighteen of the 36 (50%) neonate *S. jarrovii* were infested by ectoparasites (Table 1). Seventeen (47%) were infested by chiggers (*Eutrombicula lipovskyana*), with a mean intensity of 6.5 ± 6.9 and a range of 1–26 chiggers per lizard. Three (8%) lizards were infested by larval *Geckobiella texana,* with a mean intensity of 3.0 ± 2.6 and a range of 1–6 mites per lizard. Adult *G. texana* were not present. Two infected lizards had concurrent infections (*E. lipovskyana* and *G. texana*). The sample of 19 male and 17 female lizards contained 11 infested males (58%) and 7 infested females (41%). There was no statistical difference in rate of ectoparasite infestation between males and females (chi square = 1.0, 1 df, $P > .05$). Likewise, there was no statistical difference in intensity of infestation between male and female lizards (Kruskal-Wallis statistic = 0.46, 1 df, $P > .05$; *E. lipovskyana* and *G. texana* combined). Mean intensities were 5.7 ± 6.3 for infested males and 8.14 ± 9.20 for infested females.

Eutrombicula lipovskyana was found most frequently within skin folds on both ventrolateral surfaces of the neck (the mite pockets of Arnold 1986), but they were occasionally encountered in other areas of the body. *Geckobiella texana* was taken from the hind legs only. Representative specimens were deposited

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TABLE 1. Infestation of neonate *Sceloporus jarrovii* by ectoparasites.

SVL	N	# with *Eutrombicula lipovskyana* (#, intensity of chiggers per lizard)	# with *Geckobiella texana* (#, intensity of mites per lizard)
26	1	0	0
27	2	1 (26)	0
28	7	4 (5, 2, 1, 1)	0
29	3	1 (3)	1 (1)
30	8	4 (13, 8, 7, 2)	1 (2)
31	7	3 (6, 3, 2)	0
32	5	2 (2, 1)	0
33	2	1 (16)	0
34	0	—	—
35	0	—	—
36	1	1 (13)	1 (6)

in the U.S. National Parasite Collection (Beltsville, Maryland 20705) as U.S. National Helminthological Collection Nos. 81992 and 82077 for *E. lipovskyana* and *G. texana*, respectively.

Neonates born in captivity averaged 28.03 ± 0.98 mm SVL and ranged from 26 to 30 mm (Goldberg 1970). Thus, we estimate our field-collected sample to range from 1 day (those of 26–30 mm SVL) to 2 weeks (36 mm SVL) of age. It would appear that infestation can occur during the first few days of life, indeed, perhaps even on the day of birth (Table 1). To our knowledge, this is the only report indicating when ectoparasitic infestation may first occur in the life history of lizards. The correlation coefficient (R) between SVL and number of mites was 0.16, suggesting to us that infestation of neonates by mites is opportunistic and can occur at any time after birth. Loomis and Stephens (1973) noted that hatchling *Uta stansburiana* from Joshua Tree National Monument, California, had very few chiggers attached but acquired more mites as they grew. They gave no estimate of age when infestation might first occur. *Sceloporus jarrovii* neonates grow rapidly, many of them reaching sexual maturity by autumn when they are 5 months of age and average 54 mm SVL (Ballinger 1973). We cannot speculate on the infestation of older juvenile *S. jarrovii* since seasonal occurrence and abundance of *E. lipovskyana* are yet to be determined.

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SEASONAL VARIATION AND DIET SELECTION FROM PELLET REMAINS OF SHORT-EARED OWLS (*ASIO FLAMMEUS*) IN WYOMING

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Key words: Short-eared Owls, Asio flammeus, *diet selection, predators, Wyoming.*

Short-eared Owls (*Asio flammeus*) are medium-sized predators of open country, sage flats, grasslands, and roadsides. Often active well after sunrise, they are more diurnal than other owls in northwest Wyoming (Karulus and Eckert 1974, Clark 1985). Their foraging areas significantly overlap those of both smaller and larger owls, namely Great Horned Owls (*Bubo virginianus*) and Burrowing Owls (*Speotyto cunicularia*) (E. Stone unpublished data, Karulus and Eckert 1974). Prey sources, including small mammals, birds, and insects, are diverse and overlap those used by Great Horned Owls.

This study examines shifts in prey sources through the breeding season by identifying prey remains in Short-eared Owl pellets from wild birds. Shifts in prey sources may be the result of changes in prey abundance or availability, or competition with other owl species for the same resources. Additionally, shifts may result from changes in dietary requirements of adults or their developing dependent offspring. In this study we sought to describe whether shifts in diet occurred and, if so, what types. This descriptive study may serve as a useful baseline of data upon which future studies can be based.

METHODS AND STUDY AREA

The Short-eared Owl study area was an old irrigation ditch located approximately 2.2 km southwest of the Teton Science School in Grand Teton National Park, Wyoming. Short-eared Owl pellets were located by searching on the ground and at the base of willows (*Salix* sp.), mountain alder (*Alnus tenuifolia*), aspen (*Populus tremuloides*), and narrowleaf cottonwood (*Populus angustifolia*). One active nest was located within 20 m of the ditch and another within 2 km. We observed as many as four owls roosting along the ditch, either on the ground, in the shade of trees, or perched on the lower branches.

At the end of each month (March–October) all pellets were collected at the study site. Thus, each group of pellets collected and their contents could be assumed to have originated during that month. Short-eared Owls were no longer seen in the study area in late October and were presumed to have migrated to areas with ample winter prey, shallower snowpack, or both. Owls were first seen using the roost site in early March. To assure large enough sample sizes, we combined sample months into the following seasonal groups: spring (March, April, and May), summer (June and July), and fall (August, September, and October).

Prey items were identified using skull and teeth parts found in individual pellets. Pellet remains of *Microtus montanus* and *M. longicaudus* were not distinguishable by skull or teeth parts and were combined into a prey category hereafter referred to as *M. mont-long.*

RESULTS

Short-eared Owl pellets contained 11 different prey items. Of these, the 6 most common prey types constituted 94.42% of the diet. A significant decline in sage voles (*Lagurus curtatus*) in the fall diet of Short-eared Owls was augmented by an increase in the proportions of northern pocket gophers (*Thymomys talpoides*) and southern red-backed voles (*Clethrionomys gapperi*) (Table 1). The complete disappearance of *L. curtatus* in fall, with increases in both the number and proportion

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TABLE 1. Seasonal percentages of prey items found in Short-eared Owl pellets.

Prey type	Mar-Apr-May	Jun-July	Aug-Sep-Oct	Totals
Microtus mont-long	41.37	46.15	42.28	42.92
Thymomys talpoides	10.34	17.31	27.64*	21.03
Peromyscus maniculatus	24.14	17.31	16.26	18.45
Lagurus curtatus	13.79	13.46	0.00*	6.44
Clethrionomys gapperi	1.72	3.85	8.13*	5.58
Sorex sp.	3.45	0.00	2.44	2.15
Zapus princeps	3.45	1.92	0.00	1.29
Tamias minimus	0.00	0.00	0.81	0.43
Microtus pennsylvanicus	0.00	0.00	0.81	0.43
Unknown bird	0.00	0.00	0.81	0.43
Unidentified beetle	0.00	0.00	0.81	0.43
NUMBER OF PREY ITEMS	58	52	123	233

*Significant increase or decrease in diet ($P < .05$, chi-square post-hoc cell contributions).

of *T. talpoides* and *C. gapperi* in the diet of Short-eared Owls, represents a significant seasonal change in overall diet selection or foraging locations.

DISCUSSION

Short-eared Owl's significant seasonal variation in prey selection may be reflective of changes in the availability of their prey. Sagebrush voles (*Lagurus curtatus*) are reported to become inactive during dry periods corresponding to late summer and fall in western Wyoming (Clark and Stromberg 1987:177). Declines in prey such as *L. curtatus*, found in open areas containing sage or grassland habitats, may indicate that Short-eared Owls forage more in forest edges or under tree canopies during the latter part of the summer. These habitats are where *M. montanus*, *M. longicaudus*, and *C. gapperi* are found. *T. talpoides*, which also increased in the diet later in the season, is found in a variety of habitats with loose soil (Clark and Stromberg 1987).

In Grand Teton National Park and elsewhere, there is strong evidence that small mammal prey availability is dependent on environmental factors and climate (Pinter 1988). In 1993, one year later, a continuation of this study was planned. However, a sudden and prolonged period of warm temperatures resulted in rapid snowmelts and subsequent flooding of the subnivean environment (personal observation). Population studies of small mammals being conducted in the same area found that 1993 summer populations were the lowest recorded in 25 years of monitoring (A. Pinter personal communication).

In 1993 Short-eared Owls were first seen at the study area on 15 March but were absent for the duration of the summer. It was assumed that the owls moved their foraging and breeding activities to areas that were not affected by the subnivean flooding and depression of small mammal populations. These observations and the results of more normal years suggest that Short-eared Owls possess the flexibility to shift diets and foraging areas with changing seasonal or annual prey availability.

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HABITAT REQUIREMENTS FOR *ERIGERON KACHINENSIS*, A RARE ENDEMIC OF THE COLORADO PLATEAU

Loreen Allphin[1] and Kimball T. Harper[2]

ABSTRACT.—*Erigeron kachinensis* is a rare endemic of the Colorado Plateau in southeastern Utah. This perennial composite grows in small, isolated populations at seeps and alcoves arising along canyon walls in Cedar Mesa Sandstone substrates. Characteristics of six *Erigeron kachinensis* sites in Natural Bridges National Monument, San Juan County, Utah, were studied to determine habitat requirements for this species. Sites were analyzed with respect to geology, soil chemistry, physical properties, and vegetational characteristics. The alcoves studied were very saline, often with soil surfaces covered with a white crust of salt. Living cover was enhanced by perennially moist soils, diminished amounts of solar radiation, soil salinity, and above-average amounts of available soil phosphorus. Kachina daisy vegetative growth appears to be favored by these same abiotic factors. The most commonly associated plant species on *E. kachinensis* sites were *Aquilegia micrantha, Calamagrostis scopulorum, Zigadenus vaginatus*, and *Erigeron kachinensis.* These species and the daisy accounted for more than 75% of the total living cover in the alcoves studied. A principal components analysis procedure was developed for evaluating site suitability for *Erigeron kachinensis*. This daisy has been successfully introduced to a site selected using that model.

Key words: Erigeron kachinensis, *Colorado Plateau, critical habitat.*

The Kachina daisy (*Erigeron kachinensis* Welsh & Moore) was discovered and named in 1968 (Welsh and Moore 1968). It is a rare perennial composite of the Colorado Plateau region of Utah and Colorado. The species grows in small, isolated populations at seeps and alcoves arising along the edges of deep canyons in these areas. No discussions of the habitat requirements of this species have appeared in the literature. The Kachina daisy was proposed as "endangered" by the U.S. Fish and Wildlife Service on 16 June 1976 (U.S. Department of Interior 1975, 1976). Later proposals downgraded the original recommendation to "threatened" status for the species (U.S. Department of Interior 1988). Currently, the Kachina daisy is listed by the U.S. Fish and Wildlife Service as a category 2 species, i.e., a species for which more information is needed before assigning final designation (endangered, threatened, or sensitive).

In 1984 an effort was launched to document locations of all populations of the Kachina daisy and their size in Natural Bridges National Monument (NBNM), San Juan County, Utah. In that study eight populations were recorded (Fagan 1984). In 1988 and 1989 the National Park Service selected four of the eight populations for a 2-year monitoring program. Relative cover of Kachina daisy plants in these populations was reported to vary by almost 60% between years (Belnap 1988, 1989). Belnap's report to the National Park Service called for protection and further research to determine whether the observed declines in population size were due to natural fluctuations in temperature and precipitation or to more permanent stresses in the physicochemical environment. It was also considered possible that the species was poorly adapted to the associated environmental conditions.

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Since this species appears to be restricted to seeps and alcoves, typically along a single seepline within a canyon, there is concern for its preservation. If drought caused seeplines occupied by this species to dry up, many populations could be eliminated. As tourism increases in the canyon regions of southeastern Utah, so does the threat of human impacts on rare species. Tourists hiking in canyon bottoms look to shady alcoves as refuge from the hot summer sun. Many of the seeps and alcoves contain small, prehistoric Anasazi Indian ruins that also attract tourists.

At the outset of this study, the Kachina daisy was known only from NBNM and a population in Montrose County, Colorado. With but few known populations confined to uncommon site situations, resource managers were concerned that the species might be vulnerable to extinction. These concerns resulted in the research presented in this manuscript. Our objectives were to determine habitat requirements for the Kachina daisy and to develop a management strategy for preservation of the species. If habitat requirements can be established accurately, potentially occupiable sites for the species could be identified and new populations established.

STUDY AREA AND METHODS

The Kachina daisy grows in seeps and natural alcoves in the Cedar Mesa Sandstone of White and Armstrong canyons in NBNM between 1680 and 1890 m elevation. The Cedar Mesa Formation, deposited in Permian time (Hintze 1975), is a coarse-grained, porous sandstone that stores considerable water within its massive deposits. In thickness the Cedar Mesa Formation varies from 500 to 1200 m. Its depth is at a maximum in the Elk Ridge and NBNM area. Alcoves where the daisy grows are developed in Cedar Mesa Sandstone immediately above the Halgaito Formation.

The Halgaito Formation lies below the Cedar Mesa Sandstone. It is a part of the Cutler group, as is the Cedar Mesa Sandstone. The Halgaito Formation consists of mostly reddish brown siltstone, sandstone, and thin beds of limestone. It varies from 400 to 500 m in thickness (Hintze 1975). Where percolating water encounters finer-textured lamina in the Cedar Mesa Sandstone, it accumulates and moves laterally until it reaches the faces of vertical walls of deep, narrow drainage channels that cross outcrops of the Cedar Mesa Formation.

A survey of canyons surrounding NBNM for *Erigeron kachinensis* was initiated under a contract with the Bureau of Land Management. In addition to populations known in NBNM (Welsh et al. 1987), the Kachina daisy has now been found on lands administered by the Bureau of Land Management (Allphin and Harper 1991). Populations are known in Fish, Arch, White, and Birch canyons; from Dark Canyon Primitive Area in San Juan County, Utah; and from the lower portion of Coyote Wash, Montrose County, Colorado (Welsh et al. 1987, Allphin and Harper 1991).

Six of the eight populations in NBNM were chosen for detailed study based on accessibility and contrasting site characteristics (Fig. 1). The six study sites vary in respect to aspect, soil moisture, and soil salinity. These sites include two west-facing, two south-facing, and two north-facing alcoves. All study sites are located along the 1768-m (5800-ft) contour line. Study sites were monitored in June 1990, 1991, and 1992. It is pertinent to note that all sites occur in alcoves or seeps except site 2, which occupies a slope kept moist by seepage from an alcove directly above.

At each site individual daisy plants were selected for study using the point center quarter method (Cottam and Curtis 1956) along a 100-m transect. These individuals were marked with numbered aluminum tags held at their bases with galvanized nails. The tags facilitated later relocation of individual plants.

Several abiotic characteristics were described by taking composite soil samples from the six study populations. A minimum of five composite soil samples were taken per alcove. From those soil samples, soil water content,

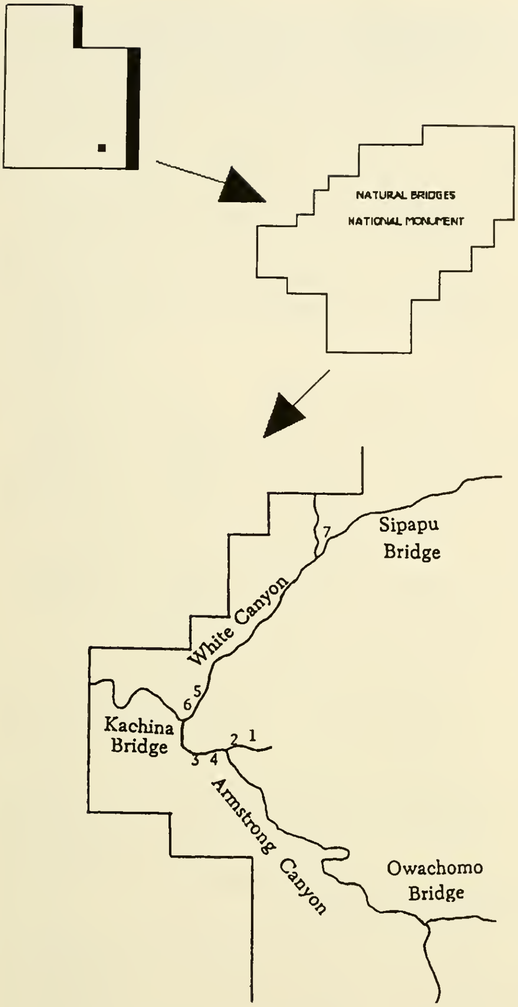

Fig. 1. Location of Kachina daisy sites monitored in this study and a site where Kachina daisy plants have been transplanted in Natural Bridges National Monument, San Juan County, Utah (# 1 = north-facing alcove A, # 2 = north-facing alcove B, # 3 = south-facing alcove A, # 4 = south-facing alcove B, # 5 = west-facing alcove A, # 6 = west-facing alcove B, and # 7 = transplant site).

percentage of coarse material (diameter >2 mm), soil texture, percentage of sand, percentage of organic matter, pH, electrical conductivity, and concentrations of the biogenic elements (P, K, Ca, Mg, Na, Cu, Fe, Mn, and Zn) were estimated. All soil analyses were made by personnel of the Soil and Plant Analysis Laboratory, Department of Agronomy and Horticulture, Brigham Young University, and all analytical methods were based on those recommended by Black et al. (1965). Soil texture was determined with a hydrometer. Reaction (pH) of soil was taken with a glass electrode on a saturated soil-water paste. Organic matter was quantitated by digestion with 1.0 N potassium dichromate. Phosphorus was determined with the iron-TCA-molybdate method on a soil extract taken with .2 N acetic acid. Exchangeable bases were freed from the soil with 1.0 N ammonium chloride. Ion concentrations in extract solutions were estimated by atomic absorption.

Vegetational data were also collected at each study site in NBNM. Frequency and cover of individual species and percentage of total living plant cover were determined for each study site using a 100-cm^2 quadrat. In addition, vegetative and floral characteristics of 600 tagged plants were recorded at each visit. Variables evaluated for each plant include number of rosettes, crown diameter, leaf length (average for two longest leaves), number of leaves, number of flower heads, number of flowers per head, and number of filled seeds per flower head. The number of filled seeds per head was determined by harvesting mature heads in June and observing whether seeds were filled with mature embryos.

Soil data from the various study sites were analyzed by one-way analysis of variance (ANOVA) for significant differences between sites. The least significant difference multiple range test of Snedecor and Cochran (1967) was used to determine significant differences among individual means for each site. Vegetational data were analyzed using a two-way analysis of variance for both site and year. Once again the multiple range test was used to identify significant differences among means for all measured vegetative characteristics among the six alcoves. ANOVAs were performed using the STATA statistical package (Computing Resource Center 1992).

To determine the effect of the abiotic environment on vegetative growth in alcoves containing the Kachina daisy, abiotic environmental variables were regressed against total living cover, species richness, and Kachina daisy characteristics. Since no significant regression correlations could be found between abiotic environmental and individual daisy characteristics, a whole-plant response index was determined using standardized values for various daisy characteristics among the six alcoves.

Vegetative daisy characteristics were standardized by setting the largest value for each variable at 100 and expressing the value for that parameter at each study site as a percentage of the maximum value. These standardized values were summed for each of the alcoves to give an integrated estimate of overall plant response. A reproductive daisy response was also measured as number of filled seeds based upon total number of heads produced by individual daisy plants and number of flowers per head. Both simple and multiple linear regressions were performed to evaluate the response of various plant variables to the following abiotic factors: moisture content, salinity, and available phosphorus in the soil. All regressions were performed using the STATA statistical package (Computing Resource Center 1992).

Composite soil samples were also taken from populations found on lands administered by the Bureau of Land Management. Species found in association with the Kachina daisy were recorded for each population. An alcove found near Sipapu Bridge within NBNM contained no Kachina daisies but did harbor several of the species commonly associated with the daisy (Fig. 1). This location was considered a potential introduction site for the Kachina daisy. A composite soil sample from the site was analyzed to further assess its suitability for this daisy. Mean soil characteristics from sites on BLM lands and the potential transplant site were analyzed by multiple range comparison with the six study alcoves. Principal components analysis (Pielou 1984)) was used to further evaluate the suitability of the Sipapu Bridge site for the Kachina daisy using all environmental variables in a multivariate analysis. Soil characteristics considered in that analysis included phosphorus (mg/kg), electrical conductivity, average soil moisture (June), and average soil temperature (June). Total species richness at each site was also used in the principal components analysis. The principal components analysis was conducted using the SAS statistical package (SAS Institute, Inc. 1993).

Demography and reproductive biology of the Kachina daisy are addressed in greater detail in another manuscript. Results presented in this paper will deal only with information concerning habitat of the species.

RESULTS

Physical Environment

Soils in alcoves occupied by Kachina daisy are sandy loams ranging from 70.4 to 89.6% sand (Table 1). They are very alkaline with pH values of 7.8–9.1. All alcoves studied develop a crusty layer of white salt on the soil surface during the drier part of the year. Data demonstrate that *E. kachinensis* is very tolerant of saline conditions. Electroconductivity of soils from the study sites ranges from 6 to 31 mmhos/cm. The average electrical conductivity value for soils from the six alcoves was 13.6 mmhos/cm. Conductivity values over 8 mmhos/cm are considered high enough to restrict yield of most crop plants (Richards 1954).

Soil temperatures (at ~1 cm depth) at sites occupied by the daisy are cool, ranging from 13.2 to 15.8° C in June (Table 1). Soils in alcoves are always cooler than surrounding soils because they receive less sunlight and stay reasonably moist. Soil temperatures in June vary only slightly among sites, with higher temperatures occurring at sites receiving greater amounts of direct sunlight.

Percent soil water content in occupied alcoves varies from 5.8 to 25.6% of dry weight in mid-June (Table 1). NBNM receives most of its precipitation from November through March (Fig. 2; Brough et al. 1987). Water accumulates in the sandstone during these months but is available for plant growth in all seasons because of the large reservoir of water held in the sandstone.

Alcoves 3 and 6 have the wettest soils (Table 1). This is perhaps related to the fact that these alcoves receive only about 1 h of direct sunlight per day in June. Site 2 has the driest soil. It occurs on a slope outside and directly below an alcove seep. In addition, it receives the most sunlight daily and is farther from a seepline than other study sites. It faces north and is exposed to sunlight only during afternoon hours.

All alcoves considered had similar levels of phosphorus (7.5–11.4 mg/kg). They also had high values for potassium, calcium, magnesium, and sodium (Table 1). ANOVA and multiple range tests demonstrate that soils at alcove 3 differ significantly from those of other alcoves. Alcove 3 soils have significantly higher electrical conductivity, a greater percentage of Na saturation, and significantly higher levels of potassium, magnesium, and sodium. This alcove also has significantly lower levels of manganese and calcium than the other alcoves studied. These differences may be related to

TABLE 1. Chemical and physical characteristics of soil from alcoves that support *Erigeron kachinensis* at Natural Bridges National Monument (1–6), San Juan County, Utah. Each value represents an average of five samples from each alcove. Alcove 7 represents potential transplant site in Natural Bridges National Monument. Column 8 represents a mean of five alcoves in surrounding canyons on BLM land. Means followed by the same letter do not differ at the $p <$ .05 level of significance. Soil temperature and moisture values represent average conditions for mid-June in summers of 1990–92.

	Alcove no.							
	1	2	3	4	5	6	7	8
Elevation (m)	1768	1768	1768	1768	1768	1768	1768	1859
Aspect (deg.)	302(WNW)	328(NNW)	160(SSE)	197(SSW)	252(WSW)	225(SW)	250(WSW)	191(SSW)
Hr. direct sunlight/day in June	5.0	5.75	1.0	4.5–5.25	4.6	0–1.5	—	—
Texture	sandy lm	loamy snd	sandy lm	sandy lm	sandy lm	sandy lm	sandy lm	sandy lm
Sand (%)	89.6 a	76.7 a	80.3 a	70.4 a	80.1 a	71.7 a	73.3 a	66.8 a
pH	8.6 c	8.8 cd	9.1 d	8.6 c	7.9 ab	7.8 a	8.6 c	8.2 b
EC (mmhos/cm)	13.1 bc	17.1 c	31.1 d	7.6 ab	6.9 a	6.0 a	—	9.8 b
Ave. soil temp (C)	14.1 a	15.8 bc	13.9 a	15.1 b	13.9 a	13.2 a	13.5 a	16.4 c
Soil moisture (%)	12.3 b	5.8 a	18.4 c	12.2 b	12.7 b	25.6 d	13.2 b	12.3 b
Organic matter (%)	1.8 b	1.1 a	2.0 bc	2.2 c	0.8 a	1.6 b	—	—
Skeletal mtl. (% by wt.)	12.1 ab	15.1 b	17.2 b	6.8 a	7.2 ab	7.2 ab	—	—
				Essential elements				
P (mg/kg)	11.4 a	10.7 a	9.8 a	10.9 a	7.5 a	8.0 a	9.3 a	10.2 a
K (mg/kg)	197.0 ab	229.5 b	640.2 c	153.0 a	80.4 a	82.0 a	—	—
Ca (mg/kg)	9590 c	7886 b	6758 a	10508 d	10884 d	10282 cd	—	—
Mg (mg/kg)	2498 a	2754 a	11904 b	2030 a	870 a	730 a	—	—
Na (mg/kg)	649.0 ab	822.4 b	2535.0 c	322.6 ab	126.7 a	127.4 a	—	—
Cu (mg/kg)	0.48 ab	0.36 a	0.56 b	0.32 a	0.36 a	0.60 b	—	—
Fe (mg/kg)	1.8 b	0.96 a	1.4 ab	1.9 b	1.9 b	2.2 b	—	—
Mn(mg/kg)	6.8 c	6.0 bc	1.8 a	6.6 c	2.4 a	4.8 b	—	—
Zn (mg/kg)	0.60 b	0.44 a	0.72 b	0.88 c	0.96 c	0.72 b	—	—
Na saturation (%) of exchangeable bases	2.5 b	3.5 bc	6.0 c	1.2 ab	0.5 a	0.6 a	—	—

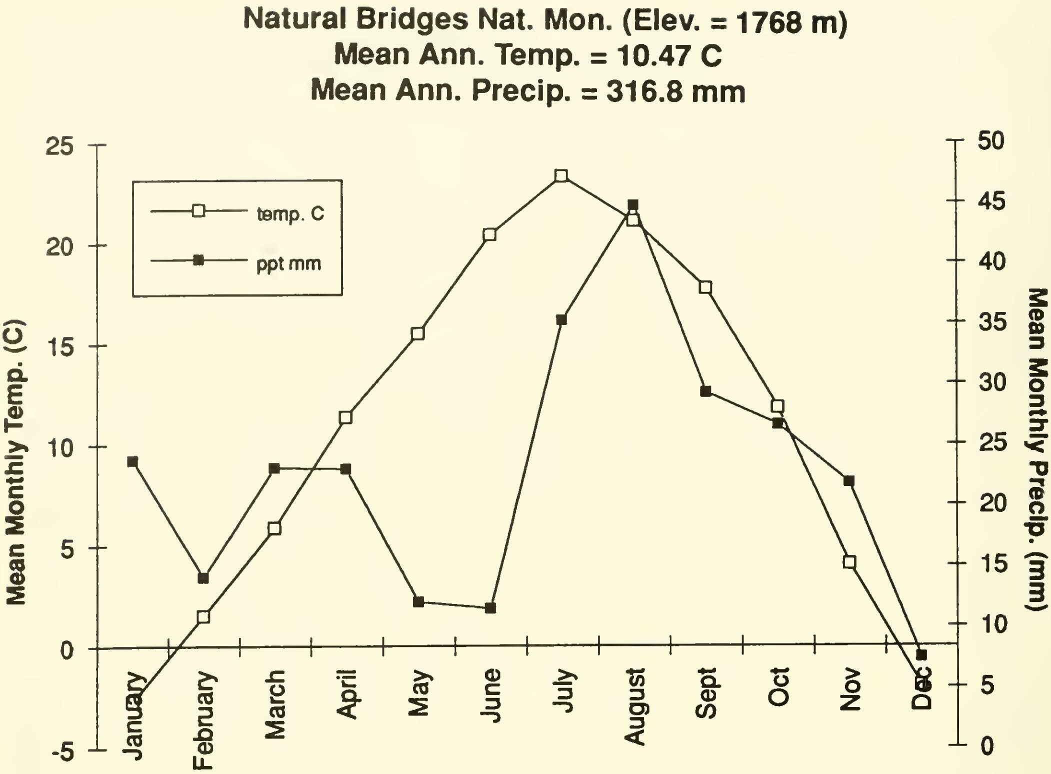

Fig. 2. Climatic diagram for Natural Bridges National Monument. Data represent average values for the period 1987–91.

the fact that the floor of alcove 3 is developed from a reddish brown siltstone/sandstone probably of the Halgaito Formation rather than the Cedar Mesa Sandstone. Even though alcove 3 soils differ from those of other alcoves, the daisy population is thriving and seems unaffected by soil differences.

Kachina Daisy Characteristics

Characteristics of the average daisy in each of the alcoves studied intensively are noted in Table 2. The average number of rosettes per individual varied from 1.4 to 2.5 among the six sites. Statistical differences among the sites with respect to the number of rosettes per daisy plant are noted in Table 2. Alcoves 3 and 4 supported the largest plants, while the smallest plants grew in alcoves 2 and 5.

Average clump diameter for the Kachina daisy ranged from 3.6 to 7.3 cm among the study sites. Alcove 2 plants had the smallest diameters, which perhaps reflects the fact that alcove 2 had the driest soil observed among the alcoves (Table 2).

Average leaf lengths ranged from 1.9 to 3.6 cm among the six study sites. Alcove 2 plants had the smallest leaves observed. Average number of leaves per plant ranged from 9.9 to 23.6 among the study sites. As might have been expected, the number of leaves per plant was smallest for alcove 2 (Table 2).

Statistical differences seen among characteristics of plants from these alcoves reflect the fact that alcoves were chosen for apparent differences in moisture, aspect, and direct sunlight. Plants from alcoves that receive little direct sunlight (sites 3, 4, and 6; Table 1) had larger leaves and clump diameters than plants from alcoves 1 and 5, which received more sunlight. The amount of sunlight could also be expected to affect soil moisture, which should also produce differences in vegetative characteristics.

Biotic Associates

Ecological and vegetational characteristics showed no significant differences among the years of study (1990–92); thus, data given in

TABLE 2. Ecological and vegetational characteristics and average characteristics of 100 randomly selected Kachina daisy plants at each of the six alcoves shown in Table 1. All values are based on data taken during field seasons 1990–92. Means followed by the same letter do not differ significantly at $p < .05$.

	Alcove no.					
	1	2	3	4	5	6
Total living cover (%)	42.5 c	17.8 a	45.5 c	62.4 d	18.1 a	37.7 b
Species richness*	6.3 a	5.3 b	4.7 c	9.0 d	4.3 c	7.0 e
Ave. # spec./ 100-cm^2 quad.	2.8 d	1.8 b	1.6 ab	2.6 d	1.4 a	2.1 c
Characteristics of *E. kachinensis*						
No. rosettes/plant	1.6 a	1.4 a	2.5 c	2.1 b	1.6 a	1.9 b
Plant diam. (cm)	4.8 b	3.6 a	6.2 c	7.3 d	4.4 b	6.6 c
Leaf length (cm)	2.7 b	1.9 a	2.5 b	3.6 c	2.1 a	3.4 c
No. leaves/plant	13.2 b	9.9 a	23.6 d	22.2 d	13.5 b	17.3 c
Plant response indices**	492 (veg.) 225 (rep.)	355 (veg.) 202 (rep.)	540 (veg.) 253 (rep.)	605 (veg.) 290 (rep.)	387 (veg.) 226 (rep.)	604 (veg.) 226 (rep.)
Characteristics of prevalent species						
Erigeron kachinensis frequency (%)***	66.7 d	44.0 b	38.7 a	54.7 c	53.3 c	72.0 e
Ave. cover (%)	6.3 b	2.9 a	7.5 c	7.0 c	3.4 a	6.0 b
No. plants/m^2	15.1	12.7	6.1	15.7	7.9	27.4
Aquilegia micrantha frequency (%)***	73.3 d	56.0 c	57.3 c	26.7 b	8.0 a	56.0 c
Ave. cover (%)	18.2 d	8.7 b	16.2 c	2.9 a	2.5 a	17.3 cd
Calamagrostis scopulorum frequency (%)***	40.0 d	16.0 b	32.0 c	40.0 d	9.3 a	41.3 d
Ave. cover (%)	4.6 b	2.7 a	16.8 d	15.0 d	2.2 a	8.1 c
Zigadenus vaginatus frequency (%)***	53.3 c	33.3 b	30.7 b	61.3 d	68.0 d	2.7 a
Ave. cover (%)	10.6 c	2.97 b	4.7 b	22.4 d	10.0 c	0.05 a

*Species richness = number of species per 25-m transect.

**Plant response indices = summed, relativized values for both vegetative (veg.) and reproductive (rep.) characteristics of the Kachina daisy (see text for details).

***Frequency = percentage of 100-cm^2 sampling quadrats placed per 25-m transect that included this species.

Table 1 are means based on results for the three summers. Total living cover at locations that support *E. kachinensis* ranged from 17.8 to 62.4% in the six alcoves studied intensively (Table 2). Most living cover was contributed by *E. kachinensis*, *Aquilegia micrantha*, *Calamagrostis scopulorum*, and *Zigadenus vaginatus*. Frequency and cover values for those species are reported in Table 2.

Several species were found to occur regularly with the Kachina daisy in both Natural Bridges National Monument and lands managed by the Bureau of Land Management in that part of San Juan County, Utah (Table 3). Considering all known locations for the Kachina daisy in San Juan County, Utah, only four species were found to coexist with it at 75% or more of the occupied sites. Those species were *Aquilegia micrantha*, *Calamagrostis scopulorum*, *Cirsium calcareum*, and *Zigadenus vaginatus*. These species are thus good indicators of habitat suitable for the Kachina daisy.

Three abiotic variables were found to have a significant effect on total living cover in the

TABLE 3. Species associated with _Erigeron kachinensis_ at all (100+) sites of occupancy on Bureau of Land Management Lands and the six study sites at Natural Bridges National Monument, San Juan County, Utah.

Aquilegia micrantha****
Calamagrostis scopulorum****
Cirsium calcareum****
Zigadenus vaginatus****
Epipactus gigantus***
Helianthella microcephala***
Heterotheca villosa***
Adiatum capillus var. _veneris_**
Carex aurea**
Castilleja linariifolia**
Cirsium rydbergii**
Gilia subnuda**
Hymenopapus filifolius var. _cinereus_**
Mimulus eastwoodii**
Senecio multilobatus**
Swertia radiata**
Galium multiflorum var. _coloradoense_*
Gilia congesta var. _palmifrons_*
Habenaria sparsiflora var. _sparsiflora_*
_Juncus arcticus_*
_Leptodactylon pungens_*
_Solidago sparsiflora_*
Aster chilensis~
Comandra unbellata~
Penstemon watsonii~
Ranunculus cymbalaria~

Trees and shrubs
Pinus edulis***
Rhamnus betulaefolia***
Cercocarpus intricatus**
_Juniperus osteosperma_*
_Pinus ponderosa_*
Amelanchier utahensis~
Clematis ligusticifolia~
Mahonia fremontii~
Populus fremontii~
Salix exigua~

****>75% of Kachina daisy populations.
***50–75% of Kachina daisy populations.
**25–50% of Kachina daisy populations.
*5–25% of Kachina daisy populations.
~<5% of Kachina daisy populations.

six alcoves: soil water content, soil salinity, and available phosphorus. Results of regression analyses between these three important environmental variables and total living plant cover, integrated vegetative response of the Kachina daisy, and species richness are reported in Table 4.

Salinity was negatively related to total living cover and species richness in simple regression analyses. Total available phosphorus was significantly related to total living cover in the alcoves. When soil salinity and soil water content were considered together in multiple regression, they were significantly correlated with total living plant cover. Partial correlation coefficients show that soil water content accounts for significantly more of the variation in total living plant cover in the model than does soil salinity [% total cover = 3.6(% water content) +.015 (EC)]. The combined effects of soil moisture, soil salinity, and available phosphorus gave the strongest multiple correlation coefficient obtained with total living cover. In this study increased soil moisture appeared to reduce the effect of salinity on plants in the alcoves and permitted good growth of most adapted species in soils of high salinity.

Vegetative response of the daisy was found to be significantly influenced by percent soil moisture (Table 4), but salinity and phosphorus were not significantly correlated with vegetative response. When salinity and moisture are combined in multiple linear regression, a positive, but not significant, influence is shown for vegetative growth. By adding phosphorus to salinity and moisture in multiple regression analysis, the correlation coefficient became statistically significant. Not only do these three abiotic variables affect total cover of all species, but they also appear to be important for vegetative growth of the Kachina daisy. In contrast, reproductive response of the daisy was not found to be significantly influenced by any abiotic variable or combination of variables. Kachina daisy reproduction by seed thus appears to be tolerant of the differences observed for important abiotic environmental variables in this study.

The Sipapu Bridge site (site 7, which did not support a population of the Kachina daisy) was found to be environmentally similar to the six Kachina daisy study sites and sites that supported the daisy on lands administered by the BLM (Table 1). Results of a principal components analysis that considered all environmental variables simultaneously confirm this finding (Fig. 3). The Sipapu Bridge site falls among the alcoves that supported Kachina daisy in the diagram depicting the principal components analysis results.

DISCUSSION

Characteristics of habitat suitable for the Kachina daisy can be predicted from the results of this study. Sites favorable for daisy growth have sandy loam soils, saline soils (13–14 mmhos/cm on average), and a perennial

TABLE 4. Influence of three important environmental variables (soil water content, soil salinity, and available phosphorus) on total living plant cover, integrated vegetative response, and species richness. Vegetative daisy response is based upon summed relativized values for leaf length, crown diameter, number of rosettes per plant, number of leaves per plant, total daisy cover, daisy density, and daisy frequency. Reproductive daisy response represents number of filled seeds per flower head, considering total number of heads per plant and total number of flowers per head. Significance level is given next to each *r*-value.

Independent variable(s)	Dependent variables			
	% living cover	Daisy response		Species richness
		Vegetat.	Reprod.	
	r-value for simple regression			
Soil water content (%)	.15 NS	.85**	.50 NS	.11 NS
Salinity (EC)	–.79*	.09 NS	.42 NS	–.75*
Available P (mg/kg)	.75*	.05 NS	.03 NS	.14 N
	Multiple *r*-value for multiple regression			
Soil water content and salinity (EC)	.95**	.75 NS	.43 NS	.79 NS
Soil water content, salinity (EC), and available P (mg/kg)	.99**	.98**	.60 NS	.86 NS

**Regression significant at $p < .05$ level of significance.
*Regression significant at $p < .10$ level of significance.
NS Regression not significant.

source of water. Occupied soils are alkaline to strongly alkaline. Kachina daisies require perennially moist, cool soils along seeplines. However, these areas typically have large overhangs that sometimes provide too much shade for adequate growth. Therefore, daisies commonly grow on the outside perimeter of the alcove or sometimes directly below the alcove, as seen at site 2. Vegetative features of the plant at sites that typically receive little direct sunlight are typical of those of shade plants: large, thin leaves and elongated stems. Soil water content appears to buffer the effect of high salinity on vegetative growth within the alcoves (Table 4). Above-average levels of soil phosphorus appear to enhance growth of the Kachina daisy (Table 4). Available soil phosphorus averaged about 9.5 mg/kg at sites occupied by Kachina daisy in this study. Habitat occupied by Kachina daisy also supports several other characteristic species. The most common species associated with the daisy include *Aquilegia micrantha*, *Calamagrostis scopulorum*, *Cirsium calcareum*, and *Zigadenus vaginatus* (Table 3).

Three abiotic variables appear to have the greatest influence on total living plant cover in alcoves and vegetative Kachina daisy growth, i.e., soil water content, soil salinity, and available soil phosphorus (Table 4). These variables obviously act in concert to influence plant growth in the alcoves. For instance, soil water content has a strong, positive effect on vegetative growth of the daisy, but the positive effect is amplified when both water and soil phosphorus are considered in the analysis (Table 4). Although these variables are important to vegetative growth in the alcoves, they appear to have minimal influence on reproduction in the Kachina daisy.

Since we observed no significant variation in Kachina daisy populations in the six alcoves studied over a 3-year period, it is questionable whether the large year-to-year variations in relative cover of this species reported by Belnap (1988, 1989) are real. Belnap's results may be attributable to the taking of samples at different locations within the alcoves in different years. Our study included three of the same alcoves as those sampled by Belnap (our alcoves 1, 5, and 6), but we could detect no significant differences in either water flow or plant community composition among years of observation. The discrepancy between Belnap's results and ours probably relates to sampling design. Our samples were always taken at the

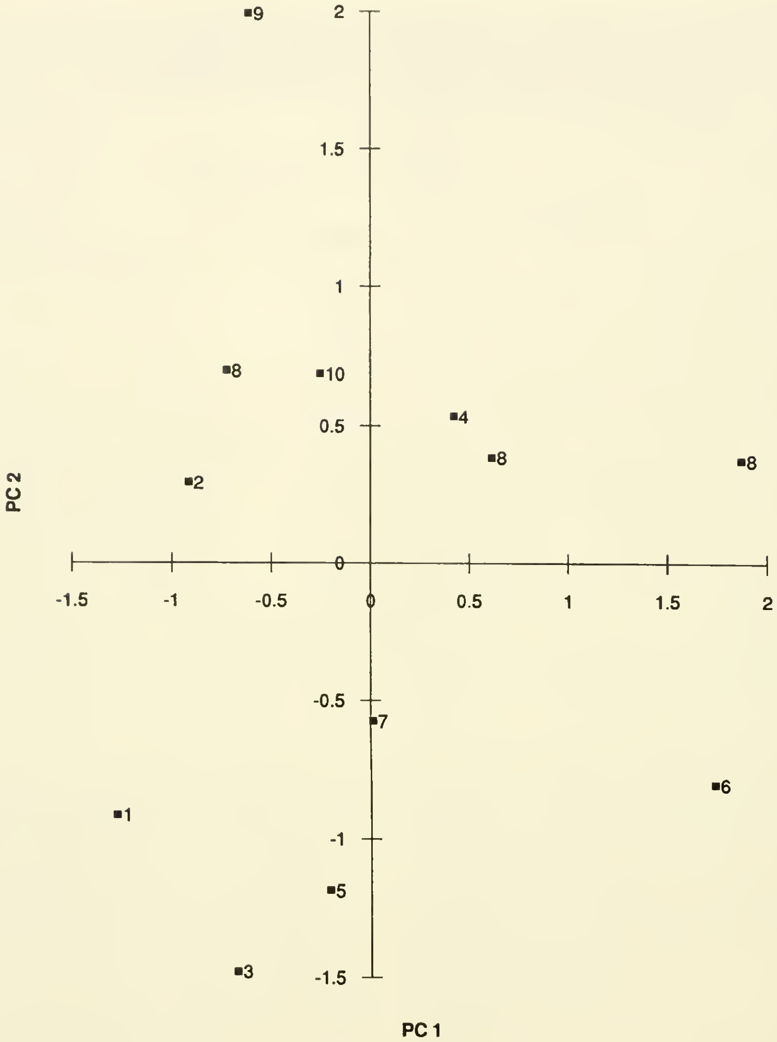

Fig. 3. Plot of the first two components of soil samples from the six Kachina daisy study sites in NBNM (1–6), the Sipapu Bridge transplant site (7), and Kachina daisy sites on BLM land (8–10, three site 8 alcoves in Fish Canyon, site 9 in White Canyon, site 10 in Arch Canyon). See Table 1 and text for explanation.

same permanently marked points in each year of study, while Belnap sampled at random within the 2 years of analysis.

The U.S. Park Service has encouraged attempts to transplant the Kachina daisy into what may be suitable habitat in NBNM, but until the results reported here became available there were no criteria for evaluating the suitability of a site for the species. Since an alcove at the Sipapu Bridge at NBNM appeared to fall within the range of environmental suitability for this daisy (Table 1, Fig. 3), we made experimental transplants of the species into that alcove. Presently, no known natural populations of Kachina daisy occur near this site. The site is a west-facing alcove along the 1768-m (5800-ft) contour level. The habitat resembles other Kachina daisy sites in that salinity is high and many species occur on the site that are known to consistently grow with the daisy. Six daisies were transplanted in the alcove in summer 1991. Four of the six survived to summer 1992. Approximately 200 plants were taken from a site to be destroyed by road construction in 1992 and transplanted at the Sipapu alcove; at least 100 of these plants survived and some even flowered in 1993. Based on these favorable results, the Park Service is now considering seeding the Kachina daisy in other suitable alcoves within NBNM.

The validity of the suite of characters given above as descriptors of suitable Kachina daisy habitat is further supported by the fact that many new locations for the species were located on BLM lands in the region by searching for habitats and associated species closely similar to the combination of characteristics noted above.

We note that others have collected an *Erigeron* from rock crevices on Elk Ridge, San Juan County, Utah, that is morphologically indistinguishable from populations in this report. However, the habitats associated with specimens from Elk Ridge rock faces and those associated with alcove daisies of the deep canyons of NBNM are extremely different in respect to elevation, soil moisture, solar radiation, soil salinity, and associated species. Genetic analysis will be required to determine how closely allied these two taxa are.

The populations found on BLM land as a result of this study demonstrate that the Kachina daisy is more common than once believed. The species is well adapted to alcoves of the Cedar Mesa Formation, but it is apparently unable to occupy any other habitats in the deep canyon environments. It is imperative that managers protect alcoves with perennial seep lines in the Cedar Mesa Formation from disturbance. Trails should not be permitted to intrude into the alcoves, and camping within the alcoves should be forbidden.

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COORDINATION OF BRANCH ORIENTATION AND PHOTOSYNTHETIC PHYSIOLOGY IN THE JOSHUA TREE (*YUCCA BREVIFOLIA*)

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ABSTRACT.—Despite the profusion of light in deserts, morphological adaptations to increase light interception are common among desert plants. We studied branch orientation and related physiological parameters in the Mojave Desert Joshua tree, *Yucca brevifolia* (Agavaceae). Azimuth and inclination were measured on all leaf rosettes of 44 *Y. brevifolia* trees. Interception of solar radiation was modeled for leaves in hypothetical rosettes facing due south and due north in December, March, and June. Carbon isotope discrimination, nitrogen content, and conductance to water vapor were measured in leaves from north- and south-facing rosettes. Rosette azimuths were nonrandom; rosettes predominantly faced southeast. North-facing rosettes were more steeply inclined than those facing south. The preponderance of south-facing rosettes reduces self-shading and increases interception of solar radiation during the winter–spring growth period. Stomatal conductance was higher for leaves in south-facing than in north-facing rosettes. Nevertheless, discrimination against ^{13}C was less in leaves of south-facing rosettes, indicating that average intercellular CO_2 concentration was also lower. South-facing whorls had higher leaf nitrogen content. Greater allocation of nitrogen to leaves in south-facing whorls probably results in those leaves having a greater photosynthetic capacity than their north-facing counterparts. Orientation of rosettes to increase interception of sunlight during the period most favorable for photosynthesis, coupled with allocation of nutrients to maintain a higher photosynthetic capacity in those rosettes, should significantly increase whole-plant carbon gain in *Y. brevifolia*.

Key words: Yucca brevifolia, *Joshua tree, carbon isotope discrimination, photosynthetic capacity, branch orientation, rosette azimuth, morphological adaptations.*

Morphological adaptations to the light environment are common among desert plants (Ehleringer and Werk 1986). The angle and inclination of leaves (Ehleringer 1988, Neufeld et al. 1988) or cladodes (Nobel 1980, 1981, 1982) may increase interception of solar radiation when air temperatures and evaporative gradients are moderate (e.g., early in the day or during winter months) and reduce incident solar radiation during hotter parts of the day or year. Neufeld et al. (1988) reported that foliage clusters in creosote bush (*Larrea tridentata*), a long-lived evergreen shrub of the Mojave and Chihuahuan deserts, are inclined from 33° to 71° and oriented predominantly toward the southeast. They suggested that such architecture would tend to minimize self-shading and maximize carbon gain during periods most favorable for photosynthesis, which could result in improved water-use efficiency. We wondered if similar morphological adaptations might be found in the Joshua tree (*Yucca brevifolia*), a long-lived arborescent monocot with evergreen leaves.

Yucca brevifolia is restricted to the Mojave Desert, where it often occurs with *L. tridentata*. Its tough, fibrous leaves grow in symmetrical whorls forming cylindrical rosettes at the end of branches (Fig. 1A). The axis of newly expanding leaves at the top of a rosette is parallel with that of the rosette. As leaves mature and become photosynthetically active, they reflex away from the branch axis so that the adaxial surfaces of the youngest fully expanded leaves are at about 55° from the rosette axis. This angle gradually increases along the rosette axis so that the oldest photosynthetically active leaves are nearly perpendicular to the rosette axis (J. Anderson unpublished data; cf. Smith et al. 1983).

Rosettes vary from about 0.2 to >1.5 m in length and typically contain 200–>1000 leaves. Young trees possess a single vertical rosette of leaves. Older trees have multiple branches that result from dichotomous branching at the apices of rosettes (Fig. 1B). Old trees can have over 100 branches and grow to >5 m in height (J. Anderson and N. Huntly unpublished data).

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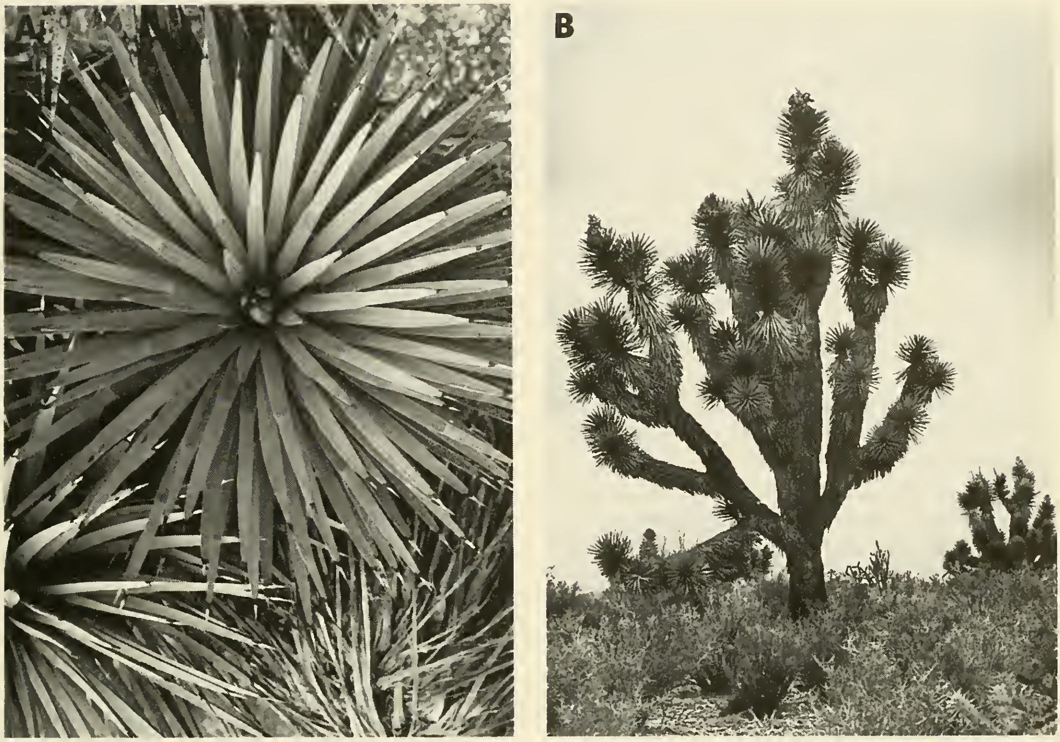

Fig. 1. (A) Cylindrical rosette of *Yucca brevifolia* leaves consisting of a sequence of whorls in which adjacent whorls are non-overlapping; (B) mature individual of *Y. brevifolia* with multiple branches.

Yucca brevifolia is a C_3 species with modest photosynthetic rates (Smith et al. 1983). Photosynthesis is light saturated at a relatively low photosynthetic photon flux density (PFD) of 400–600 μmol m^{-2} s^{-1}; the nonoverlapping leaf arrangement results in a relatively even distribution of light throughout the rosette. Smith et al. (1983) found that stomatal conductances are highest during the winter–spring wet season and predicted that 80% of the annual photosynthetic productivity would occur from January through May. During the dry season, conductances are reduced to a very modest peak early in the morning. Thus, like *L. tridentata* and most aridland plants, Joshua trees live in an environment where opportunities for carbon gain are constrained, both seasonally and diurnally.

We tested the hypothesis that leaf rosettes are distributed nonrandomly within crowns of *Y. brevifolia*. After documenting a strong tendency for southeasterly orientation of rosettes, we compared leaf nitrogen content and carbon isotope discrimination (△) of rosettes on south vs. north sides of trees. Finally, we used porometry to explore the significance of differences in nitrogen allocation and △. We show that nonrandom orientation of photosynthetic leaf rosettes in *Y. brevifolia* is closely integrated with physiology.

STUDY AREA

The study was conducted at Lytle Ranch Preserve, 48 km west of St. George, Utah (37°9′N, 114°1′W, elevation 850 m), during March of 1989 and 1991. Lytle Ranch is in the northeastern Mojave Desert near the northern distributional limit of *Y. brevifolia*. Extensive *Yucca* woodlands occur on benches adjacent to Beaver Dam Wash. Other common species on the benches are *Coleogyne ramosissima*, *Ambrosia dumosa*, *Larrea tridentata*, *Thamnosma montana*, and *Krameria grayi*. Average annual temperature and precipitation at St. George are 16.5°C and 209 mm, respectively.

METHODS

Orientation of rosettes was assessed for 44 trees chosen systematically at 15-m intervals along permanently marked transects on two benches. Each tree had fewer than 60 branches, and we measured azimuth and inclination of all branches on every tree. Azimuth was measured clockwise from true north to the nearest degree with a compass by sighting along the longitudinal axis of each rosette. Inclination of the rosette axis from horizontal was determined using an angle gauge with a built-in level.

Carbon isotope composition and total leaf nitrogen were measured in leaves collected in March 1989 from eight trees on the permanent transects. On each tree one fully expanded young leaf was taken from a rosette pointing due south, and a paired leaf sample was taken from a rosette pointing due north. Samples were dried and ground and then submitted to the Stable Isotope Research Facility for Environmental Research at the University of Utah for determination of carbon isotope ratios. Total leaf nitrogen was determined on subsamples of the paired leaf samples with a LECO C-H-N analyzer at the Holm Research Center, University of Idaho.

Carbon isotope discrimination (△) was calculated from the carbon isotope ratios according to Farquhar and Richards (1984), assuming that the isotopic composition of the air was –7.8^{o}/oo. Carbon isotope discrimination is related linearly to the intercellular concentration of CO_2 (c_i):

$$\triangle = a + (b - a)(c_i/c_a) \qquad (1)$$

where a is the discrimination against $^{13}CO_2$ relative to $^{12}CO_2$ associated with diffusion in air (4.4^{o}/oo), b is discrimination against the heavy isotope by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (27^{o}/oo), and c_a is the concentration of CO_2 in the atmosphere (about 350 μL L^{-1}). Because b, a, and c_a are usually constant, variation in △ reflects variation in c_i/c_a, which results from variation in stomatal conductance and in demand for CO_2 by the photosynthetic apparatus (Farquhar et al. 1982). Equation 1 was used to estimate c_i for leaves in north- and south-facing rosettes.

We measured leaf conductance to water vapor (g_w) on 21 and 22 March 1991 with a LI-COR 1600 steady-state porometer. On both days a high cloud cover was present from dawn until dusk, which blocked direct sunlight and created uniform light conditions on all sides of the trees. Nine trees in the vicinity of the permanent transects, each having at least two north-facing and two south-facing rosettes, were chosen for sampling. A fully expanded leaf near the apex of the rosette was sampled in each of two rosettes on the north and south sides of each tree. Means of the two measurements were used for statistical analyses. A preliminary sample indicated that conductances of abaxial and adaxial leaf surfaces were similar, as reported by Smith et al. (1983); so, for convenience in holding the porometer in place, we sampled only adaxial surfaces. Paired measurements were made from north- and south-facing rosettes on the nine trees between 0900 and 1200 h (MDT). Photosynthetic photon flux density (PFD) was measured with a LI-COR 170 quantum sensor (LI-COR, Inc., Lincoln, Nebraska, USA). PFD varied from 200 to 800 μmol m^{-2} s^{-1} during the measurement periods, but for the paired sample on each tree PFD was essentially constant and equal on both sides of the tree.

Because of the complexity of the architecture of *Y. brevifolia* (Fig. 1B), it was beyond the scope of this study to model light interception of whole trees, taking into consideration shading by other branches and self-shading within rosettes. Instead, we predicted the incident PFD for leaves in rosettes on the south and north sides of trees for 22 December, 21 March, and 21 June. Solar azimuths and inclinations for those dates at the latitude of Lytle Ranch were calculated according to Ehleringer (1989b). We calculated the cosine of the angle of incidence (cos i), the fraction of the direct beam of solar radiation that is intercepted by a leaf, for leaves in hypothetical rosettes facing either due south or due north and having an inclination of 60°. Excluding trees with only one branch, this was the mean inclination of the population. Cos i was calculated for four leaves per hypothetical rosette: leaves on the top and bottom, with their axes perpendicular to the ground, and leaves on both sides, with their axes parallel to the ground. Because of the symmetry of whorls of leaves in rosettes (Fig. 1A), estimates of incident radiation for those four leaves should be proportional to that for an entire rosette. We assumed that leaves were planar and that each leaf was inserted at an angle of 55° from the rosette axis, the mean value for the youngest fully expanded leaves on several trees. Cos i was calculated for both surfaces of each leaf (i.e., when cos i was negative, indicating that light would strike the abaxial side of a leaf, the absolute value was used). Thus, estimates of incident PFD include both abaxial and adaxial surfaces of the four leaves. Direct solar beam PFD values were predicted from a polynomial regression equation based on actual PFD measurements made throughout a clear day in mid-March at Lytle Ranch. Direct-beam PFD estimates were multiplied by cos i of each hypothetical leaf for a given date/time to estimate incident PFD. Those values were averaged for the four leaves as an index of incident PFD for the hypothetical rosettes.

Statistics were calculated according to Zar (1984). Mean azimuths and inclinations were calculated trigonometrically for individual trees, and those means were used to calculate a grand mean for all trees. Uniformity of leaf whorl azimuths within each tree was tested with the Watson U2 statistic. A chi-square goodness-of-fit statistic was used to test for random distribution of whorl azimuths pooled for all trees sampled using twelve 30° classes. Association between azimuth and inclination was tested using a two-way contingency table, with inclinations and azimuths grouped in 30° classes. Paired *t* tests were used to determine whether △, total leaf nitrogen, or g_W differed between the south and north sides of the trees.

RESULTS

Rosette azimuths within trees having more than four branches (the minimum required for the Watson U2 test) were not distributed randomly ($P < .001$ in all 23 cases). Azimuths for individual branches (pooled for all trees) fell predominantly between 90° and 270° (Fig. 2A); this distribution was also nonrandom ($X^2 = 78.13$, d.f. = 11, $P < .001$). All mean rosette azimuths for trees with two or more branches fell between 90° and 280°, with one exception that had a mean azimuth of 10° (Fig. 2B). Mean azimuths of individual trees were tightly clustered around the grand mean of the population, 163° (angular deviation s = 42, $n = 44$; Fig. 2B).

The mean inclination of rosettes on trees having two or more branches fell between 42° and 82° from the horizontal. Trees with two to five branches had more steeply inclined rosettes than did trees with six or more branches. Inclination was associated with azimuth ($X^2 = 39.45$, d.f. = 22, $P < .025$); rosettes having northerly azimuths (170°–90°) were more steeply inclined than those with southerly azimuths (Fig. 3).

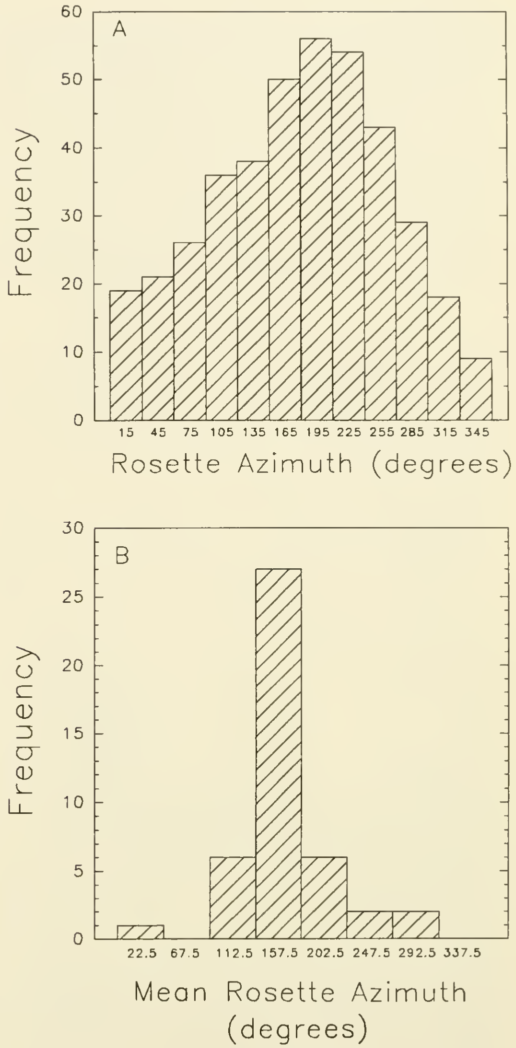

Fig. 2. Frequency distributions of leaf rosette azimuths for 44 *Yucca brevifolia* trees at Lytle Ranch Preserve, Utah: (A) distribution for all branches; and (B) distribution for the means of individual trees.

Simulation of light interception shows that leaves in rosettes facing south would intercept substantially more direct sunlight than those in rosettes facing north at all times of year, but the difference is much larger in winter and spring than in summer (Fig. 4). When sun

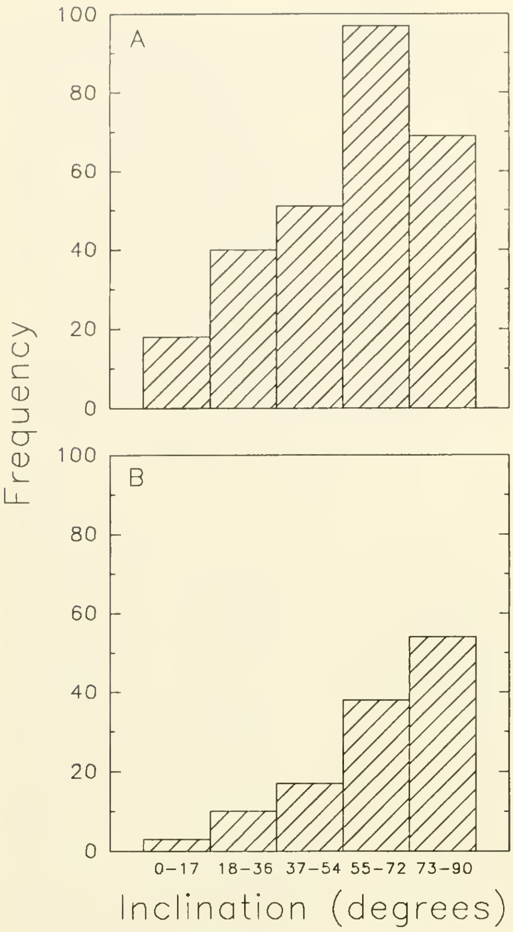

Fig. 3. Frequency distributions for rosette inclinations for 33 *Yucca brevifolia* trees having more than two branches at Lytle Ranch Preserve, Utah: (A) distribution for rosettes in the southern 180° arc (azimuths from 90° to 270°) from the tree's trunk; (B) distribution for those in the northern 180° semicircle.

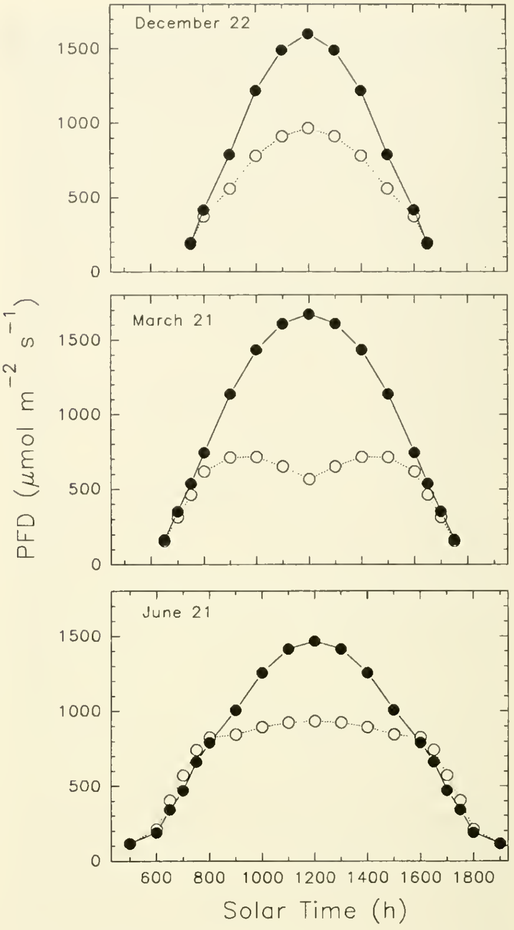

Fig. 4. Predicted diurnal patterns of direct-beam photosynthetic photon flux density (PFD) incident on leaves in hypothetical rosettes of *Yucca brevifolia* trees located at Lytle Ranch Preserve, Utah. Incident PFD was estimated for adaxial and abaxial surfaces of leaves in four positions in the rosette (see Methods) for 22 December, 21 March, and 21 June. Closed circles represent rosettes facing due south; open circles represent those facing due north.

angles are low, little direct sunlight is intercepted by abaxial surfaces of leaves in rosettes facing southeast and adaxial surfaces of leaves in rosettes facing north; those surfaces contribute more to total interception with increasing sun angles. Morning and afternoon peaks for leaves in the north-facing rosette in March are a consequence of the insertion angle (55°) for the two horizontally opposed leaves.

For the analysis shown in Figure 4, it is assumed that the four modeled leaves would be exposed to direct-beam solar radiation throughout the day. Clearly, that assumption would not hold for all leaves at all times of day. Because of the low density of Joshua tree stands and low stature of other plants in the community, shading by other individuals occurs rarely. However, self-shading occurs among leaves within rosettes and among branches within trees. Both would be minimized for branches having southerly aspects (Geller and Nobel 1986). Smith et al. (1983) asserted that the nonoverlapping arrangement of leaves of *Y. brevifolia* resulted in effective penetration of light into a rosette from the top. Leaves in rosettes having northerly azimuths would receive more shade from the rosette in which they occur, from other branches on the same tree, and from the main trunk of the tree, based on the patterns of shadows cast by

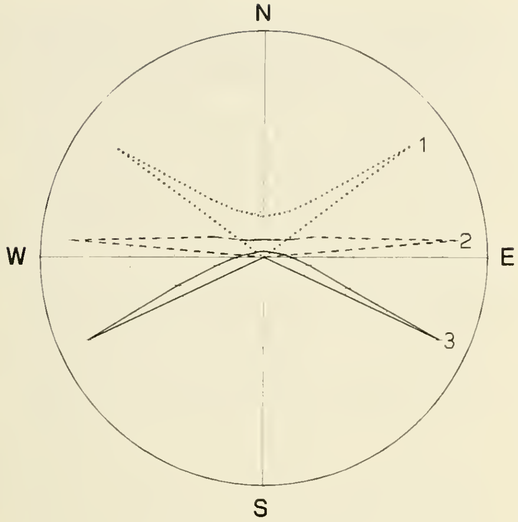

Fig. 5. Direction and length of shadows cast from early morning until late afternoon by an object 1 unit in height (1 unit = distance between concentric dashed circles) at the latitude of Lytle Ranch Preserve, Utah, for (1) 22 December, (2) 21 March, and (3) 21 June.

an object at Lytle Ranch in December, March, and June (Fig. 5).

Carbon isotope discrimination was lower in leaves of rosettes that faced south than in leaves of rosettes that faced north (Table 1). Estimates of c_i based on these △ values were 141 μL L^{-1} for leaves in rosettes on the south side of trees and 156 μL L^{-1} for leaves in rosettes on the north side. The corresponding ratios of c_i/c_a, assuming c_a was 350 μL L^{-1}, would be 0.40 and 0.45, respectively.

Total nitrogen content of leaves in rosettes facing south was higher than that in rosettes facing north (Table 1). For seven of the eight paired samples, the estimate of total leaf nitrogen was higher for the leaf from the south-facing rosette.

Leaves in rosettes on the south side of trees had higher conductances to water vapor than did leaves on the north side (Table 1). Mean g_w was higher on the south side in each of the nine trees tested.

DISCUSSION

The distribution of rosette azimuths of *Y. brevifolia* is clearly not random; rosettes point predominantly in southerly directions. Furthermore, branches on the north side of trees tend to be more steeply inclined than those on the south, which would tend to elevate the rosettes and reduce self-shading. Rosettes on the south side intercept substantially more direct solar radiation throughout the year, and the difference is especially pronounced in winter and early spring when sun angles are relatively low (Fig. 4). It is at this time that the bulk of annual carbon gain occurs (Smith et al. 1983). Shading of leaves in north-facing rosettes also would be greatest during the winter and early spring. Self-shading would magnify differences in incident direct-beam radiation between leaves in south- vs. north-facing rosettes shown in Figure 4. Thus, a second advantage of positioning rosettes on the south side of trees is to minimize self-shading.

TABLE 1. Carbon isotope discrimination (△), leaf nitrogen content (N), and leaf conductance to water vapor (g_w) for leaves in north-facing and south-facing rosettes of *Yucca brevifolia* at Lytle Ranch Preserve, Utah.

Parameter	North-facing rosettes	South-facing rosettes	*n*	*P*[*]
△ (⁰/oo)	14.7	13.7	8	.0005
N (%)	0.91	1.02	8	.015
g_w (mol m^{-2} s^{-1})	0.125	0.155	9	.001

[*] Probability that the mean of the paired differences equals zero based on results of paired-sample *t* test.

The nonrandom branch orientation in Joshua trees appears to be closely coordinated with parameters related to photosynthetic capacity. Lower △ in leaves on the south vs. north side of trees indicates that leaves on the south operate at a lower average c_i. As shown in equation 1, △ is a time-integrated measure of c_i reflecting the importance of both stomatal limitation to diffusion of CO_2 and capacity of the mesophyll to fix CO_2 (Farquhar et al. 1982). Numerous studies have shown that instantaneous gas exchange measurements are related to △ as predicted by the theory (Hubick et al. 1986, Ehleringer et al. 1992). We found that g_w was higher in leaves of south-facing whorls, indicating that lower c_i was associated with higher g_w. Because we measured g_w under conditions when both sides of trees were equally illuminated, we assume that observed differences in g_w reflect intrinsic differences related to photosynthetic capacity. These results imply that photosynthetic capacity was higher in leaves of south-facing rosettes.

Photosynthetic capacity and Rubisco activity often are positively correlated with leaf nitrogen content (Wong et al. 1985, Field and

Mooney 1986, Evans 1989). Field (1983) predicted that net photosynthesis would be maximized if nitrogen were allocated preferentially to leaves that receive more light. This is precisely what we observed; leaves in south-facing rosettes had higher nitrogen concentrations than those from rosettes on the north side of trees. Relatively low leaf nitrogen contents of *Y. brevifolia* were in a range where any increase in nitrogen would be expected to increase photosynthetic capacity.

One might expect lower △ and lower c_i in leaves of south-facing rosettes to be a consequence of lower stomatal conductance. However, observation of the pattern found here is not without precedence. Korner et al. (1988) reported that △ decreased in plants with increasing altitude while carboxylation efficiency and stomatal conductance increased. Leaf nitrogen content also increased with altitude, which contributed to an increased photosynthetic capacity (Korner et al. 1988). Lower △ is associated with higher photosynthetic capacity in peanut cultivars (Hubick et al. 1986, Wright et al. 1993) and sunflower (G. Farquhar personal communication).

Other factors could contribute to the observed difference in △ between leaves on the north vs. south side of trees. Maximum stomatal conductance may occur at light levels somewhat below light saturation for photosynthesis, as observed in other species (e.g., Anderson 1982). Thus, leaves on the north side might receive sufficient diffuse radiation to open stomata but not saturate the photosynthetic apparatus, which could result in higher average c_i than would occur if photosynthetic tissues were light saturated. Also, shading typically results in near instantaneous reductions in photosynthesis, whereas conductance changes more slowly (Anderson 1982, Knapp and Smith 1987). Therefore, c_i of leaves on the north side might be higher in comparison to those on the south because those on the north experience shading more frequently, particularly during the winter–spring growing season when sun angles are relatively low.

Although differential light levels and intermittent shading may contribute directly to observed differences in c_i, the coincidence of lower c_i, higher g_w, and higher nitrogen content in leaves of south-facing rosettes provides strong evidence that the lower c_i is primarily a consequence of higher photosynthetic capacity. We conclude that differential allocation of nitrogen to leaves on the south side of Joshua trees results in substantially higher photosynthetic capacities in those leaves. This, coupled with orientation of rosettes to increase interception of sunlight during the period most favorable for photosynthesis, would enhance productivity of whole trees for a given level of nitrogen availability.

The △ values for *Y. brevifolia* are among the lowest reported for C_3 plants (cf. Ehleringer 1989a, Korner et al. 1991, Ehleringer et al. 1992). Ehleringer (1989a) reported carbon isotope ratios for desert C_3 plants corresponding to △ values ranging from 13°/oo to 23°/oo, but values for *Y. brevifolia* are generally much lower than those reported by Ehleringer et al. (1992) and Schuster et al. (1992) for desert shrubs such as *Ambrosia dumosa*, *Larrea tridentata*, and *Coleogyne ramosissima* that often occur with Joshua trees. △ is negatively correlated with water-use efficiency (Farquhar et al. 1989). Low △ values and corresponding estimates of c_i indicate that *Y. brevifolia* leaves have very low stomatal conductances relative to their photosynthetic capacities. This would translate to high water-use efficiency compared to co-occurring C_3 plants, assuming they were subjected to comparable leaf-air vapor pressure deficits.

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VARIANCE AND REPLENISHMENT OF NECTAR IN WILD AND GREENHOUSE POPULATIONS OF *MIMULUS*

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Abstract—We compared nectar production in wild populations and greenhouse-grown populations of the monkey flower species of section *Erythranthe* of the genus *Mimulus*. Nectar was sampled from over 1000 flowers. For each flower the volume of nectar was measured with a calibrated micropipette and the percentage of sugar with a hand refractometer. Percentage of sugar varied little from flower to flower in both field and greenhouse studies, but volume varied markedly from flower to flower in field studies and even more in greenhouse studies. This high variance in nectar volume appears to be intrinsic. The amount of nectar in greenhouse populations tended to increase with time in the absence of pollinators. The amount of nectar in field populations tended to remain the same with time despite withdrawals by pollinators. Thus, nectar appears to be replenished both with time and as a response to pollinator withdrawals. The latter conclusion was corroborated by sampling nectar at 2-h intervals all day and comparing the total volume produced by a flower to the volume of nectar produced in control flowers sampled only at the end of the day.

Key words: Mimulus, *nectar, nectar volume, nectar variance, nectar replenishment, pollinator reward.*

Nectar is the primary reward for the principal pollinators, hummingbirds and bumblebees, of flowers such as the monkey flowers of section *Erythranthe* of the genus *Mimulus* (Scrophulariaceae), based on our own observations and as suggested by Free (1970), Faegri and Van Der Pijl (1979), and Baker (1983). Pollen is a secondary reward, particularly for bumblebees, but the analysis of its effect on attracting pollinators was beyond the scope of this study. Here we concentrate on the nectar rewards of the species of the section.

Five of the six species of section *Erythranthe*—*Mimulus cardinalis, M. eastwoodiae, M. nelsonii, M. rupestris,* and *M. verbenaceus*—have red, tubular, hummingbird-pollinated flowers, whereas the two races of the sixth species, *M. lewisii*, have light lavender pink or deep magenta pink, open, bumblebee-pollinated flowers (Hiesey et al. 1971, Vickery 1978, Vickery and Wullstein 1987). All the species are self-compatible but usually do not self-pollinate. So, pollinators are required for normal seed set (Vickery 1990).

To characterize the nectar rewards of this group, we examined (1) the standing crop of nectar present in flowers of wild and greenhouse-grown populations of each species and (2) the ability of flowers to replenish their nectar levels.

Methods

For field studies, flowers of a population of each species and race (Table 1) were analyzed in the wild for their nectar characteristics. Nectar volume was measured with a calibrated micropipette. Percentage of sugar in the nectar was determined with a hand refractometer. Measurements were made on different fresh flowers at 2-h intervals all day from dawn to dusk (Appendix 1). Flowers were sampled destructively inasmuch as we found that merely probing the flower with a micropipette failed to remove the occasionally sizeable remainder of nectar (Table 2).

Greenhouse studies were undertaken to avoid the variable of unequal numbers of pollinator visits and variations of climate observed in studies of wild populations. Different fresh flowers of greenhouse-grown populations of each species and race (Table 1) were sampled at 2-h intervals from bud stage (bumblebees often probe and rob buds) until flowers fell or shriveled (Appendix 2). Again, flowers were sampled destructively to be comparable to field studies as well as to obtain as complete measurements of the volume and as accurate measurements of the percentage of sugar of the nectar as possible.

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TABLE 1. Localities of populations used in the study by species, population number, habitat, locality, elevation, and collector. Vouchers are in the Garret Herbarium (UT) of the University of Utah, Salt Lake City.

Mimulus cardinalis **Douglas**	
6651	Growing by stream, Bear Wallow picnic area, Santa Catalina Mtns., Pima Co., Arizona, elev. 2130 m. Collected by Charles T. Mason, Jr., 2143.
7113	Los Trancos Creek, San Mateo Co., California, elev. 40 m. Collected by Malcom Nobs February 1958.
7120	South face of San Antonio Peak, Los Angeles Co., California, elev. 2250 m. Collected by Verne Grant 9760.
13106	Growing by spring, Aguage Vargas, Cedros Island, Baja California del Norte, Mexico, elev. 600 m. Collected by Steven Sutherland 25 October 1981.
13486	Growing along road to the Pacific Ocean, ca 2 miles west of turnoff from El Camino Real, Santo Tomas, Baja California del Norte, Mexico, elev. ca 500 m. Collected by Steven Sutherland 20 February 1984.
Mimulus eastwoodiae **Rydberg**	
6079	Growing in seeps under overhanging sandstone cliffs, Bluff, San Juan Co., Utah, elev. 1415 m. Collected by R. K. Vickery, Jr., 800.
13514	Growing in seeps in sandstone shelter caves near Anasazi ruins, south side of river, Bluff, San Juan Co., Utah, elev. 1375 m. Collected by Steven Sutherland May 1985.
Mimulus lewisii **Pursh**	
5875	Growing along small stream where Patsy Morley ski trail crosses Albion Basin Road, Alta, Salt Lake Co., Utah, elev. 2680 m. Collected by R. K. Vickery, Jr., 2723.
6103	Growing along effluent stream from Ice Lake, Soda Springs, Placer Co., California, elev. 2000 m. Collected by R. K. Vickery, Jr., 1361.
13515	Smoky Jack campground, Yosemite National Park, California, elev. ca 1800 m. Collected by Steven Sutherland 24 March 1986.
Mimulus nelsonii **Grant**	
6271	Growing in and by a small brook in the pine forest on Devil's Backbone, Sierra Madre Occidental, Durango, Mexico, elev. 2555 m. Collected by R. K. Vickery, Jr., 2614.
Mimulus rupestris **Greene**	
9102	Growing on moist, conglomerate cliff, ca 100 m below the Tepozteco Temple, Tepoztlan, Morelos, Mexico, elev. 2300 m. Collected by R. K. Vickery, Jr., 2738.
Mimulus verbenaceus	
5924	Growing by Bright Angel Creek near Phantom Ranch, Grand Canyon, Arizona, elev. 612 m. Collected by Earl Jackson November 1954.
13518B	Growing near stream, Oak Creek Canyon, Coccino Co., Arizona, elev. ca 1800 m. Collected by Steven Sutherland April 1985.
13547	Growing by spring emerging from a talus slope at base of red sandstone canyon wall, Vassey's Paradise, below Lee's Ferry, Grand Canyon, Arizona, elev. 1015 m. Collected by Steven Sutherland 20 April 1986.

Wild and greenhouse nectar studies suggested to us that nectar replacement might occur in response to removal of nectar by pollinators. So, nectar volume and percentage of sugar were measured repeatedly on flowers of greenhouse-grown populations. Flowers were gently probed (not destructively sampled) with micropipettes. Each flower was probed every 2 h from 0800 to 1600 h, nectar characteristics recorded, and nectar volumes summed (Appendix 3). At 1600 h previously unsampled control flowers were gently probed in the same manner and nectar characteristics recorded for comparison to the repeatedly sampled flowers (Appendix 3). *Mimulus* flowers of section *Erythranthe* typically develop in pairs at each node of the flower stem, except in *M. eastwoodiae* and *M. rupestris.* One flower was repeatedly sampled and the other used as the control wherever possible. Occasionally, fluctuating asymmetry between members of a pair led to one flower developing more rapidly than the other. Usually the flowers developed synchronously and to the same size as Møller and Pomiankowski (in press) suggest for developmentally stable, pollinator-visited flowers such as *Mimulus.* It was important to use flowers of the same size and developmental stage inasmuch as they produce more nectar than smaller flowers of pairs exhibiting fluctuating asymmetry (Møller and Pomiankowski in press)

For the statistical analyses two tests were employed. *F*-tests were used to compare variances of the pairs of wild populations and greenhouse populations for nectar volumes

TABLE 2. Comparison of nectar volume obtained by probing the flower vs. volumes obtained by destructively sampling the flower. Flowers were probed with a micropipette and then destructively sampled to obtain the remainder of nectar present. Greenhouse-grown plants were used.

	#1 flower		#2		#3		#4		#5		Volume
	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	$\bar{x}$
M. cardinalis–7113											
initial probe	7.0	24.5	3.0	24.5	0.0	0.0	2.0	21.4	5.5	16.0	8.4
remainder	0.8	29.0	0.5	20.6	0.0	0.0	0.0	0.0	0.5	14.0	0.4
M. cardinalis–7120											
initial probe	7.0	17.1	9.0	19.1	6.5	18.8	8.5	17.0	9.0	7.0	8.0
remainder	12.0	17.2	26.0	19.4	17.0	19.0	14.0	17.1	26.0	7.7	19.0
M. cardinalis–6651											
initial probe	6.0	14.0	6.0	18.6	3.0	20.2	0.2	10.0	—	—	3.8
remainder	5.5	14.0	8.5	18.6	0.2	17.0	4.0	20.5	—	—	4.5
M. eastwoodiae–6079											
initial probe	0.0	0.0	1.0	25.0	0.5	34.0	7.0	17.0	7.0	14.0	3.1
remainder	0.8	21.2	0.0	0.0	1.0	27.4	3.5	17.0	5.0	14.0	2.0
M. lewisii–6103											
initial probe	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
remainder	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
M. lewisii–5875											
initial probe	0.0	0.0	0.7	15.3	0.7	10.6	0.8	8.0	0.8	29.2	0.6
remainder	0.1	26.0	0.3	14.0	0.0	0.0	0.0	0.0	0.2	29.0	0.1
M. nelsonii–6271											
initial probe	7.0	16.3	4.7	18.8	8.5	16.0	1.2	14.0	—	—	5.4
remainder	12.5	16.2	1.6	19.0	1.0	16.0	1.4	13.2	—	—	4.1
M. rupestris–9102											
initial probe	0.0	0.0	1.0	34.0	2.2	25.2	0.0	0.0	0.0	0.0	0.6
remainder	0.0	0.0	0.8	29.2	1.5	25.6	3.0	25.8	5.5	28.1	2.1
M. verbenaceus–5924											
initial probe	7.0	24.5	3.0	24.5	0.0	0.0	2.0	21.4	5.5	16.0	3.5
remainder	0.8	29.0	0.5	20.6	0.0	0.0	0.0	0.0	0.5	14.0	0.4

and sugar concentrations (Tables 3, 4). The *F*-test is particularly suitable to test variances (Sokal and Rohlf 1981). The null hypothesis was that observed variances of the wild and greenhouse populations sampled the same statistical population. The *F*-test was also used to compare nectar volumes and sugar concentrations at successive 2-h intervals during the day. The Tukey-Kramer procedure (Lehman et al. 1989) was used to compare nectar volumes and sugar concentrations of greenhouse-grown representatives of the various species and races to each other (Table 5). This method uses average sample sizes and is to be preferred to the T′-method or GT-2 method for comparisons of unequal sample sizes, according to Sokal and Rohlf (1981).

RESULTS AND DISCUSSION

Wild Populations

Observations of the standing crop of nectar in flowers of wild populations revealed significant differences in nectar volumes but not sugar concentrations among some populations but not others (Tables 3, 4, 5). *Mimulus lewisii* (both races), *M. rupestris*, and *M. eastwoodiae* formed one group with low nectar volumes that were insignificantly different from each other. *Mimulus nelsonii* and *M. cardinalis* formed a second group with significantly higher volumes. *Mimulus verbenaceus* bridged the two groups with intermediate nectar volumes. In general, the more tubular and brighter red the flowers, the greater the volume of nectar and the more frequent the visits by hummingbirds, although this varied from population to population and locality to locality. Conversely, the more open and pinker the flowers, the less the volume of nectar and the more frequent the visits of bumble or carpenter bees.

Despite general trends, actual numbers of pollinator visits to flowers of wild populations varied markedly. Specifically, in an average of 3 h of observation each of *M. rupestris* (9102), *M. cardinalis* (13106), and *M. eastwoodiae* (6079), no pollinator visits were observed at all. In 2 h of observations each of *M. verbenaceus* (13518B) and *M. nelsonii* (6271) 3 and 7 visits, respectively, by hummingbirds were

TABLE 3. Summary of nectar volumes (standing crops) produced by flowers of wild populations and greenhouse-grown populations of the species of section *Erythranthe.* ↑ = significantly higher variance and ↓ = significantly lower variance in the greenhouse-grown population than in the wild population.

Wild populations				Greenhouse populations[a]				Variances equal	
Population number (Table 1)	Sample size (*n*)	Mean volume (μl)	Standard deviation	Population number	Sample size (*n*)	Mean volume (μl)	Standard deviation	*F* ratio	Probability
M. cardinalis									
13486	80	12.08 ± 1.34	± 11.00	*13106*	40	50.78 ± 1.89	± 13.71	1.7330	.1906
M. eastwoodiae									
13514	88	1.10 ± 0.17	± 1.16	*6079*	27	6.41 ± 0.31	± 2.58	45.1157	.0000 ↑
M. lewisii—Sierra Nevada race									
13515	69	0.60 ± 0.21	± 0.63	*6103*	22	2.29 ± 0.38	± 3.52	41.5997	.0000 ↑
M. lewisii—Rocky Mountain race									
5875	121	0.97 ± 0.07	± 0.74	*5875*	127	1.54 ± 0.07	± 0.81	0.7317	.3932
M. nelsonii									
6271	155	16.10 ± 1.16	± 15.39	*6271*	38	19.26 ± 2.34	± 9.44	4.5126	.0349 ↑
M. rupestris									
9102	13	0.99 ± 0.78	± 1.54	*9102*	55	5.42 ± 0.38	± 3.02	7.0458	.0099 ↓
M. verbenaceus									
13518B	65	7.27 ± 1.21	± 6.05	*13547*	43	42.49 ± 1.49	± 13.67	29.4422	.0000 ↓

[a] Values for nectar volumes in unopened buds (see Appendix 2) are omitted from these data.

recorded but no bee visits. In the populations of *M. lewisii,* 7 hummingbird and 232 bumblebee visits were observed in 13 1/2 h of observations of population 13513 of the Sierra Nevada race, and 2 hummingbird and 12 bumblebee visits were observed in 4 1/4 h of observation of population 5875 of the Rocky Mountain race. The highest number of pollinator visits was observed in the Santo Tomas population (13486) of *M. cardinalis* with 600+ visits by hummingbirds and 70+ visits by bumblebees in the course of 4 1/2 h of observation. All observations were made for 15-min periods scattered from dawn to dusk. Each population had at least 200 flowers in bloom. The number of pollinator visits to a population depends strongly on the guild of pollinators in that area at that time. For example, the Santa Tomas area was alive with pollinators, whereas Cedros Island lacked them almost completely.

Nectar volume varied so much from flower to flower (Appendix 1) that pollinators would have to visit each flower in order to ascertain its nectar reward. Actually, pollinators appear to be cueing in on shapes and/or colors that promise an acceptable reward, on average, but not necessarily from each flower visited. Variances were so high for nectar volumes that one standard deviation approached the population mean in magnitude in all populations (Table 3). In contrast, variation in sugar concentration was far less. It was less than one-fifth the magnitude of the mean on average (Table 4). High variances in nectar volume could be due to unequal visits by pollinators; variations in soil moisture; climatic factors such as wind, dew, or rain; or microclimatic variations in humidity around the flowers (Cruden and Hermann 1983, Wyatt et al. 1992).

As a day progressed, from as early as 0600 to as late as 2000 (Appendix 1), the mean volume of nectar in flowers of wild populations changed little despite withdrawals by pollinators, evaporation, dilution, stimulation by climatic factors (Table 6), or, possibly, by reabsorption of nectar by the nectaries (Búrquez and Corbet 1991). Specifically, the nectar volume remained essentially unchanged in flowers of four populations: *M. eastwoodiae, M. nelsonii, M. rupestris,* and *M. verbenaceus.* It decreased, as would have been anticipated for all populations, if replenishment were not occurring, in only two populations, *M. cardinalis* and the Sierra Nevada race of *M. lewisii.* It actually rose in one population, the Rocky Mountain race of *M. lewisii.* The increase in volume was

TABLE 4. Summary of nectar sugar concentrations (standing crops) produced by flowers of wild populations and greenhouse-grown populations of the species of section *Erythranthe*. ↑ = significantly higher variance and ↓ = significantly lower variance in the greenhouse-grown population than in the wild population.

Wild populations				Greenhouse populations[a]				Variances equal	
Population number (Table 1)	Sample size (*n*)	Mean concentration (%)	Standard deviation	Population number	Sample size (*n*)	Mean concentration (μl)	Standard deviation	*F* ratio	Probability
M. cardinalis									
13486	80	12.86 ± 0.42	± 3.82	*13106*	40	20.78 ± 0.59	± 3.54	0.3136	.5766
M. eastwoodiae									
13514	88	16.14 ± 0.91	± 8.90	*6079*	27	18.97 ± 1.65	± 7.27	3.4170	.0671
M. lewisii—Sierra Nevada race									
13515	69	12.07 ± 0.68	± 4.46	*6103*	22	13.72 ± 1.21	± 8.53	18.6158	.0000 ↑
M. lewisii—Rocky Mountain race									
5875	121	16.97 ± 0.93	± 8.32	*5875*	127	33.05 ± 0.90	± 11.74	12.3031	.0005 ↓
M. nelsonii									
6271	155	19.94 ± 0.33	± 3.97	*6271*	38	17.92 ± 0.66	± 4.55	0.4615	.4977
M. rupestris									
9102	13	18.98 ± 2.54	± 14.09	*9102*	55	17.53 ± 1.23	± 7.64	5.8744	.0181 ↓
M. verbenaceus									
13518B	65	14.42 ± 0.45	± 4.48	*13547*	43	17.32 ± 0.55	± 1.61	26.4864	.0000 ↑

[a] Values for sugar concentrations in unopened buds (See Appendix 2) are omitted from these data.

not due to dilution inasmuch as there was no corresponding decrease in sugar concentration (Table 6). The only species showing a decrease in sugar concentration was *M. rupestris*, which, however, showed no significant rise in nectar volume. These observations suggest to us that flowers are producing additional nectar both as the day advances and/or as pollinators remove it.

Greenhouse-grown Populations

Flowers of the greenhouse-grown populations had, as an overall average, more than three times the volume of nectar found in flowers of wild populations, but essentially the same levels of sugar concentration. In three populations, 5875 of the Rocky Mountain *M. lewisii*, 6271 of *M. nelsonii*, and 9102 of *M. rupestris* (Table 1), direct comparisons could be made between greenhouse-grown plants and plants in wild populations because greenhouse plants were either transplants or grown from seeds collected from the same wild populations. These greenhouse plants exhibited about twice the volume of nectar recorded for corresponding wild plants. In the other four populations only indirect comparisons were possible. In these cases wild populations came from similar habitats but different localities than the greenhouse-grown populations of the same species or race (Table 1). Greenhouse-grown plants exhibited over four times the volume of nectar found in their wild counterparts. Presumably the increase in nectar volume in both groups of populations when grown in the greenhouse reflects lack of nectar withdrawals in the greenhouse due to absence of pollinators and to more standardized and more consistently favorable climatic, soil moisture, and humidity conditions in the greenhouse. Higher relative humidity has been shown to lead to higher nectar production in *Ascelpias syriaca* (Wyatt et al. 1992). The increased nectar was more dilute in *Ascelpias* in contrast to the *Mimulus* nectar, which remained at essentially the same sugar concentration. Relative humidity in our greenhouse was typically 65%, but ranged up or down by 15%. Relative humidity at Moab, the closest station to our locality at Bluff, averaged 19%, with ranges of 11–80% on average (Utah Climate Center 1993). This was during July and August (1993), the *Mimulus* flowering season. It is small wonder that nectar production for that desert population rose significantly higher, nearly sixfold, in our humid greenhouse

TABLE 5. Comparisons of mean nectar volumes and mean nectar sugar concentration of the species of *Mimulus* of section *Erythranthe* using the Tukey-Kramer test (Sokal and Rohlf 1981). Positive values show pairs of means that are significantly different.

	Volume						
	nelsonii	*cardinalis*	*verbenaceus*	*eastwoodiae*	*rupestris*	*lewisii* R. Mtn.	*lewisii* Sierras
nelsonii	–5.2141						
cardinalis	–2.3365	–7.1398					
verbenaceus	1.8260	–2.8556	–9.0312				
eastwoodiae	7.9089	3.1797	–3.0400	–8.2443			
rupestris	9.5366	4.6160	–1.7667	–6.9066	–5.6009		
lewisii— R. Mtn.	8.0589	3.3297	–2.8900	–8.0943	–7.0387	–8.2443	
lewisii— Sierras	8.8322	4.0631	–2.1927	–7.3825	–6.2735	–7.5325	–7.6327

	Sugar concentration						
	nelsonii	*rupestris*	*lewisii* R. Mtn	*eastwoodiae*	*verbenaceus*	*cardinalis*	*lewisii* Sierras
nelsonii	–8.0453						
rupestris	–7.3070	–8.6421					
lewisii— R. Mtn.	–7.8996	–9.1731	–12.7208				
eastwoodiae	–5.9996	–7.2731	–10.8208	–12.7208			
verbenaceus	–5.5712	–6.8299	–10.2783	–12.1783	–13.9349		
cardinalis	–2.4944	–3.7911	–7.4909	–9.3909	–11.2158	–11.0165	
lewisii— Sierras	–2.1016	–3.3875	–7.0176	–8.9176	–10.7241	–10.5711	–11.7772

(Table 3). Relative humidity at Park City, the closest station to our Alta locality, during the July–August flowering season for *Mimulus* averaged 46% with ranges of 17–85% on average (Utah Climate Center 1993). Nectar production in the greenhouse was slightly, but insignificantly, higher than nectar production in the wild for this pair of populations. Relative humidity appears to help set the limit on how much of a flower's potential for nectar production is realized. There was no indication of nectar reabsorption.

Greenhouse populations exhibited much the same groupings of nectar volume producers as did wild populations. That is, *M. eastwoodiae, M. lewisii* (both races), and *M. rupestris,* were the low producers; *M. cardinalis* and *M. verbenaceus* were the high producers; and *M. nelsonii* was the intermediate producer.

In all but two cases variance in nectar volumes increased significantly in greenhouse-grown populations compared to wild populations (Table 6). This occurred despite lack of pollinators. Variability in the standing crop of nectar appears to be intrinsic and not simply due to uneven nectar withdrawal by pollinators. Variability in nectar volume might function as a strategy to insure pollinator visits to many flowers of a population (Wiens personal communication); that is, the psychological principle of intermittent rewards would seem to be operating (Edward Cook personal communication).

In flowers of greenhouse-grown populations sugar concentrations varied insignificantly. They tended to remain in the range of 12–20% (Appendix 2).

Nectar Replenishment

Nectar replenishment is indicated by the general maintenance of nectar volumes despite nectar removal in wild populations and by the tendency of nectar volumes to increase in the absence of pollinators in greenhouse-grown populations (Table 6).

Comparison of nectar volumes produced when flowers were probed with a micropipette every 2 h until the late afternoon—like a pollinator removing nectar—with flowers that were not probed at all until the late afternoon demonstrated that repeatedly probed flowers produced at least twice as much nectar as flowers that were probed only once (Appendix 3). While nectar volume apparently

TABLE 6. Changes in floral nectar volume (µl) and percent (%) sugar with time, during the course of a day (Appendices 1, 2). ↑ equals a significant increase with time and ↓ equals a significant decrease with time.

Species	Wild populations			Greenhouse populations		
	Mean	*F* ratio	*p*	Mean	*F* ratio	*p*
M. cardinalis						
Santo Tomas	12.0812 µl	27.5578	.0000 ↓	—	—	—
	12.8637%	0.4307	.5136	—	—	—
Cedros Island	—	—	—	50.7675 µl	1.2138	.2775
	—	—	—	20.7850%	16.9257	.0002 ↑
M. eastwoodiae						
San Juan	1.1068 µl	3.3306	.0715	—	—	—
	16.1454%	0.8536	.3581	—	—	—
Bluff	—	—	—	6.2462 µl	20.1851	.0001 ↑
	—	—	—	19.2392%	0.1186	.7334
M. lewisii—Sierra						
Yosemite	0.6028 µl	4.0774	.0475 ↓	—	—	—
	12.0753%	0.0679	.7953	—	—	—
Ice Lake	—	—	—	2.2909 µl	2.6352	.1202
				13.7272%	4.8804	.0390 ↓
M. lewisii—Rocky Mtns.						
Alta	0.9719 µl	5.1894	.0245 ↑	6.2464 µl	20.1851	.0001 ↑
	16.9743%	2.1025	.1497	19.2392%	0.1186	.7334
M. nelsonii						
Sierra Madre	16.1045 µl	0.0568	.8119	19.2657 µl	0.3331	.5674
	19.9412%	1.4890	.2243	17.9263%	5.9106	.0202 ↑
M. rupestris						
Tepozteco	0.9923 µl	0.0159	.9018	5.4163 µl	2.7497	.1032
	18.9846%	8.0010	.0164 ↓	17.5345%	1.1780	.2827
M. verbenaceus						
Oak Creek	7.2333 µl	0.8416	.3624	—	—	—
	14.3757 %	3.9155	.0521	—	—	—
Grand Canyon	—	—	—	46.3830 µl	12.0601	.0009 ↑
	—	—	—	17.8630%	19.7339	.0000 ↑

increases with time alone (see above), volume increases more rapidly with repeated removals.

The amount of nectar produced by flowers in successive 2-h periods tended to decrease in *M. cardinalis, M. eastwoodiae, M. nelsonii,* and *M. verbenaceus* (Appendix 3). The percentage of sugar dropped in only two cases, the 7120 population of *M. cardinalis* and the 6271 population of *M. nelsonii.* Apparently, production of additional nectar is not achieved, with these possible exceptions, by dilution, but reflects the actual synthesis of more nectar. Consequently, calculations of the amount of sugar produced by a flower depend not only on volume of nectar and percent sugar at the time of sampling (Bolten et al. 1979, Sutherland and Vickery 1993), but also on the amount of sampling and hence the amount of replenishment of nectar in that flower.

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(Appendices 1–3 follow on pages 220–227.)

APPENDIX 1. Standing crop of nectar in flowers of wild populations of the species and races of section *Erythranthe* of the genus *Mimulus* at different times of day. Time is given in terms of a 24-hour clock, volume of nectar is in microliters (μl), and sugar concentration of the nectar in percent sugar (%). Data were gathered by Steven Sutherland in 1986-87.

***M. cardinalis*—Santo Tomas, Baja California, del Norte, Mexico**

	0600		0800		1000		1200		1400		1600		1800		2000	
	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%
	8.5	18.0	10.0	8.0	13.5	12.2	4.0	11.6	3.0	9.0	8.0	14.8	1.0	8.0	3.0	13.0
	43.5	16.8	6.5	6.6	18.0	11.2	49.5	14.2	19.0	19.2	3.5	14.8	1.5	12.4	3.0	12.4
	46.0	16.2	16.0	12.0	7.5	14.8	8.5	20.4	8.0	9.6	1.5	9.0	1.5	16.2	22.0	13.6
	22.5	10.0	25.0	13.2	6.5	9.6	21.5	14.3	5.5	13.0	1.0	7.4	2.0	21.0	9.0	15.4
	12.0	15.6	4.5	12.2	4.0	14.0	32.5	12.8	4.0	7.6	1.0	10.4	4.0	14.2	11.5	17.2
	34.0	16.6	11.0	11.4	6.5	10.4	13.5	14.4	22.5	14.8	8.5	11.2	5.0	6.8	14.0	19.2
	13.0	12.4	35.0	14.0	7.0	9.0	3.0	11.0	21.0	23.8	7.0	8.0	4.0	5.0	6.5	17.2
	18.5	9.0	40.0	16.4	11.5	6.4	13.0	12.4	6.5	13.0	3.5	13.4	4.0	7.4	5.0	14.6
	29.0	14.0	16.0	12.2	10.0	11.2	7.0	14.2	8.0	16.8	3.5	15.4	6.0	13.4	10.5	16.4
	20.5	14.2	13.0	9.6	23.5	14.8	5.5	12.2	10.0	7.2	3.5	7.4	7.0	9.0	7.0	21.4
$\bar{x}$ =	24.8	14.3	17.7	11.6	10.8	11.4	15.8	13.8	10.8	13.4	4.1	11.2	3.6	11.3	9.2	16.0

***M. eastwoodiae*—Bluff, Utah**

	0800		1000		1200		1400		1600		1800	
	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%
	7.3	17.6	0.3	13.8	0.2	21.6	0.3	27.2	1.0	14.4	1.2	17.2
	2.0	18.2	0.9	33.0	1.3	12.4	0.4	17.0	1.2	11.8	1.2	12.8
	1.0	15.4	2.5	31.2	1.8	33.0	0.3	26.6	0.6	3.8	1.0	6.8
	0.6	7.0	2.3	11.4	0.7	18.2	0.2	5.4	0.3	2.0	2.5	12.0
	0.8	14.0	0.5	5.6	0.5	23.8	1.0	10.4	0.7	7.4	1.2	12.8
	1.3	5.2	1.4	11.2	0.6	22.4	0.3	25.2	0.6	9.2	1.3	18.6
	0.6	10.0	0.8	7.2	4.5	28.0	0.4	22.0	2.6	25.0	0.8	26.0
	0.3	10.4	1.2	8.4	2.4	17.4	1.8	9.0	0.2	7.6	0.1	9.0
	0.6	6.8	0.6	5.2	4.3	33.0	0.5	21.8	1.2	10.0	2.5	8.8
			1.3	20.2	1.2	33.0	0.4	19.0	1.8	11.2	0.6	23.0
$\bar{x}$ =	1.6	11.6	1.2	14.7	1.7	24.3	0.5	18.3	1.0	10.2	1.2	14.7

***M. lewisii*—Yosemite, California**

	0600		0800		1000		1200		1400		1600		1800	
	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%
	0.1	6.0	0.3	10.0	0.7	9.4	0.4	14.0	0.8	11.4	0.7	9.0	0.5	10.6
	3.2	10.8	1.2	10.6	1.3	10.2	1.2	14.6	0.1	7.4	0.4	9.0	1.0	12.2
	0.2	5.0	0.8	10.0	1.2	29.4	0.2	16.4	0.8	10.8	0.2	15.2	0.5	12.2
	1.4	17.4	2.0	22.6	0.5	7.0	0.1	16.2	0.2	13.2	0.1	6.0	0.3	16.8
	0.5	16.4	0.2	6.0	0.2	8.4	0.2	12.6	0.1	11.4	0.1	10.8	0.1	9.4
	0.8	20.2	0.3	10.2	1.6	26.8	0.1	14.0	0.3	12.2	0.1	4.0	0.2	15.2
	1.0	13.2	0.3	12.4	0.2	10.8	0.6	13.6	0.2	11.0	0.2	11.2	0.1	12.8
	1.0	5.2	0.3	8.6	0.4	11.0	0.1	14.0	2.7	16.8	0.1	16.0	1.5	10.8
	0.3	11.6	0.3	10.4	0.2	9.4	0.1	13.6	0.2	9.0			0.6	12.8
$\bar{x}$ =	0.9	12.0	0.7	11.3	0.8	13.1	0.3	13.9	0.5	11.1	0.2	10.3	0.6	12.6

***M. lewisii*—Alta, Utah**

	0600		0800		1000		1200		1400		1600	
	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%
	0.3	15.1	0.2	3.6	0.8	14.4	0.5	14.8	0.4	21.2	2.4	20.2
	1.1	9.2	0.1	7.6	0.8	27.2	2.2	15.2	1.7	11.0	1.4	20.4
	0.8	10.8	0.2	13.8	1.4	24.2	0.5	19.6	0.8	11.8	0.4	19.4
	2.8	15.4	0.2	7.6	0.2	9.0	0.2	6.0	1.3	10.2	1.2	20.8
	3.0	12.1	2.2	8.6	0.3	20.2	0.8	10.2	0.1	11.0	3.2	20.8
	0.7	25.8	1.0	27.2	0.9	25.0	0.5	33.0	0.2	29.2	2.0	20.8
	0.4	17.6	0.6	7.4	2.2	9.0	0.2	10.2	1.6	8.2	0.8	14.4
	0.8	20.0	0.2	12.8	2.3	16.4	1.0	15.2	0.3	33.0	1.3	21.2
	0.8	12.6	0.2	6.8	0.4	33.0	1.0	7.0	1.2	15.2	1.2	21.4
	0.6	4.0	0.3	3.3	0.9	19.2	1.5	15.0	0.6	16.0	0.4	11.0
$\bar{x}$ =	1.1	14.2	0.5	9.9	1.0	19.8	0.8	14.6	0.8	16.7	1.4	19.0

APPENDIX 1. Continued.

***M. nelsonii*—Sierra Madre Occidental, Sinaloa**

	0600		0800		1000		1200		1400		1600		1800		2000	
	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%
	12.3	18.4	32.3	21.4	12.4	16.8	10.8	16.8	2.1	17.0	5.2	20.2	12.3	18.4	32.3	21.4
	7.3	15.6	6.1	17.0	30.2	19.0	44.0	18.0	2.8	17.0	4.4	21.2	7.3	15.6	6.1	17.0
	22.0	30.4	15.0	70.2	10.6	17.0	23.6	15.2	12.0	17.6	6.2	25.4	22.0	30.7	15.0	20.2
	5.5	20.0	15.4	18.8	14.0	15.4	32.4	18.2	2.0	17.2	11.3	23.8	5.5	20.0	15.4	18.8
	2.9	16.4	27.6	16.0	11.3	15.8	22.6	16.6	2.1	25.4	2.6	20.2	2.9	16.4	27.6	16.0
	3.7	15.6	53.5	17.8	5.7	19.8	4.7	15.0	2.5	21.0	2.7	19.0	3.7	15.6	53.5	17.8
	14.6	21.6	12.7	20.0	5.8	16.8	7.3	19.4	33.2	23.4	3.4	18.2	14.6	21.6	12.7	20.0
	27.5	27.0	1.0	25.2	2.2	16.6	6.9	17.6	4.3	20.8	2.5	15.8	27.5	27.0	1.0	25.2
	10.8	21.2	10.0	18.3	2.4	16.0	12.7	17.6	14.5	29.2	3.2	23.2	10.8	21.2	10.0	18.2
	5.0	21.6	1.7	18.4			2.4	16.2	4.2	29.0	2.7	20.2	5.0	21.6	1.7	18.4
$\bar{x}$ =	11.2	20.8	17.5	19.3	11.3	17.0	16.7	17.0	8.0	21.8	4.4	20.7	11.2	20.8	17.5	19.3

***M. rupestris*—Tepozteco, Morelos**

	1000		1200		1400	
	Vol.	%	Vol.	%	Vol.	%
	0.3	20.2	0.7	14.2	5.6	22.2
	0.3	32.0	2.6	18.4	0.2	6.0
	1.3	55.2	0.3	6.0	0.3	15.2
	0.4	32.0	0.1	6.0	0.2	11.4
					0.6	8.0
$\bar{x}$ =	0.6	34.8	0.9	11.1	1.4	12.6

***M. verbenaceus*—Oak Creek Canyon, Arizona**

	0800		0900		1200		1400		1600	
	Vol.	%	Vol.	%	Vol.	%	Vol.	%	Vol.	%
	13.3	13.0	1.0	13.0	19.5	13.2	11.7	12.2	2.6	22.2
	4.3	15.0	0.2	7.0	9.7	13.2	0.7	21.2	11.4	16.8
	2.4	14.0	0.3	6.0	5.4	11.2	0.7	12.2	6.3	16.4
	14.0	17.2	4.3	11.8	18.3	12.4	2.5	12.2	2.0	12.2
	3.6	16.8	0.5	9.8	9.4	8.4	4.0	12.2	17.0	15.8
	1.8	24.4	7.4	17.4	7.8	12.4			2.4	24.0
	0.7	6.8	9.2	17.0	8.5	12.8			3.1	18.2
	1.5	12.0	5.0	16.2	10.6	25.8			10.1	10.2
	7.0	13.0	10.2	14.6	7.3	12.4			3.0	21.4
	5.2	13.2	13.4	16.4	1.6	12.4			26.8	16.8
$\bar{x}$ =	5.4	14.6	5.1	12.9	9.8	13.4	3.9	14.0	8.5	17.4

APPENDIX 2. Standing crop of nectar in flowers of greenhouse-grown populations of the species and races of section *Erythranthe* of the genus *Mimulus* at different ages. Age is given in hours (24-hour clock) before and after 0600 on the morning of bud break. Volume of nectar is in microliters (μl) and sugar concentration of the nectar in percent sugar (%).

M. cardinalis **(13106)—Cedros Island, Baja California del Norte, Mexico**

Day −1			Day +1			Day +2			Day +3			Day +4		
Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%
−18	37.4	15.8	0	53.9	16.2	24	68.8	18.2	48	30.0	19.2	72	53.9	27.4
−18	40.0	17.0	2	44.5	18.0	26	43.8	17.2	48	85.6	12.2	74	52.9	23.0
−16	18.8	15.6	4	37.1	22.2	26	22.2	17.2	50	37.8	21.6	76	52.2	29.8
−16	28.3	16.2	6	51.0	21.8	28	50.0	18.8	50	73.1	16.4	78	64.5	24.2
−14	30.8	16.2	8	50.0	18.2	28	26.9	19.2	52	66.4	17.6	80	45.6	28.0
−14	36.6	14.0	10	38.8	18.2	30	45.3	20.6	52	50.6	15.8	82	39.9	25.8
−12	22.1	16.4	10	42.3	22.6	30	59.4	22.2	54	50.8	22.2			
−12	22.1	16.4	12	61.3	18.2	32	57.6	20.0	54	31.9	22.2			
						32	43.0	21.6	56	54.7	22.2			
						34	49.4	20.6	56	51.8	21.2			
						34	35.2	21.2	58	50.0	24.2			
						36	77.9	19.0	58	69.0	24.0			
									60	64.8	23.6			
									60	46.8	19.6			
$\bar{x}$ =	29.5	16.0		47.4	19.4		48.3	19.7		54.5	20.1		51.5	26.4

M. eastwoodiae **(6079)—Bluff, Utah**

Day −1			Day +1			Day +2			Day +3			Day +4			Day +5		
Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%
−24	0.3	35.4	0	3.5	25.4	32	1.8	26.4	48	6.4	22.8	72	9.4	14.9	96	8.8	22.7
−22	1.9	28.0	4	2.9	20.0				50	5.1	14.0	74	8.0	18.6	98	10.9	20.2
−20	2.1	30.4	6	3.2	18.6				52	4.8	31.4	76	5.0	10.3	100	8.0	27.3
−18	3.5	19.4	8	4.2	21.6				54	5.3	13.4	78	5.0	8.1	100	10.0	11.3
−16	0.6	22.8	10	4.5	15.8				56	10.4	6.0	80	6.0	17.1	102	8.8	14.8
−14	0.9	47.2	12	1.8	30.2				58	7.5	13.4	82	8.4	16.4	104	2.2	33.0
−12	1.7	25.0										84	7.2	13.1	106	8.6	20.6
															108	7.2	31.3
$\bar{x}$ =	1.6	29.7		3.4	21.9		1.8	26.4		6.6	16.8		7.0	14.1		8.1	22.7

APPENDIX 2. Continued.

***M. lewisii* (6103)—Ice Lake, California**

Day −1			Day +1			Day +2			Day +3			Day +4		
Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%
−24	0.1	11.0	0	0.3	17.4	24	0.6	22.0	48	0.2	32.0	74	2.8	8.8
−22	0.1	6.0	2	0.2	7.0	26	0.4	20.8	50	0.8	12.2	82	0.2	5.0
−20	0.2	25.0	4	0.4	22.8	28	0.8	17.8	52	11.6	3.4			
−18	0.1	16.0	6	4.3	3.8	30	1.5	12.0	54	11.8	1.0			
−16	0.2	21.4	8	1.2	16.2	34	0.9	13.0	56	1.7	13.0			
−14	0.2	16.0	10	0.2	25.4	36	1.4	13.4	58	0.7	3.0			
−12	1.0	23.6	12	0.4	25.4				60	8.0	6.6			
$\bar{x}$ =	0.3	17.0		1.0	16.9		0.9	16.5		5.0	10.2		1.5	6.9

***M. lewisii* (5875)—Alta, Utah**

Day −1			Day +1			Day +2		
Age	Vol.	%	Age	Vol.	%	Age	Vol.	%
−24	0.4	24.8	0	1.4	20.0	24	3.1	24.4
−24	0.5	26.4	0	2.0	14.8	24	2.9	26.2
−22	3.7	11.0	2	0.9	20.8	26	1.9	29.4
−20	1.8	10.2	4	0.4	20.0	28	0.5	59.0
−20	1.2	10.4	4	1.8	18.0	28	1.2	43.0
−18	1.0	13.0	6	1.7	14.8	30	3.1	34.2
−18	1.2	10.2	6	1.5	26.8	30	3.3	36.6
−18	1.9	10.8	8	1.9	28.0	32	0.6	45.6
−16	2.7	16.0	8	1.2	28.2	32	0.3	48.8
−16	1.5	16.2	10	1.4	26.2	34	0.6	50.2
−14	2.6	9.4	10	1.2	34.0	34	0.6	58.8
−14	2.6	9.4	12	2.2	28.6	36	0.7	56.0
−12	2.2	11.0	12	1.8	26.2	36	0.6	51.2
−12	2.4	12.2						
$\bar{x}$ =	1.9	13.9		1.5	22.9		1.4	44.0

APPENDIX 2. Continued.

***M. nelsonii* (6271)—Sierra Madre, Durango, Mexico**

Day –1			Day +1			Day +2			Day +3			Day +4			Day +5		
Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%
–22	3.2	18.2	2	9.9	20.2	26	33.6	20.6	50	27.4	16.2	76	10.5	18.0	100	22.0	19.0
–20	0.3	22.4	4	14.5	14.0	26	13.0	19.2	50	18.4	22.4	76	10.5	18.0	102	10.6	28.0
–20	18.6	12.2	6	20.0	16.8	28	12.6	15.2	52	40.0	17.6	78	29.2	15.4			
–20	9.7	14.0	6	16.6	12.2	28	16.3	25.6	52	22.4	19.0	78	5.8	29.4			
–18	5.3	12.0	8	10.2	17.6	30	10.4	16.6	52	23.6	14.4	82	28.3	21.0			
–18	1.7	23.2	8	15.8	12.6	30	27.3	12.4	54	14.1	30.4						
–16	6.9	12.2	8	3.5	18.2	32	26.5	12.2	56	31.8	15.6						
–14	5.3	13.4	10	27.8	19.6	32	38.4	15.6	58	23.6	15.2						
			12	13.5	12.4	34	13.6	18.2									
						34	19.5	15.0									
x̄ =	6.4	16.0		14.6	16.0		21.1	17.0		25.2	18.9		15.7	19.6		16.3	23.5

***M. rupestris* (9102)—Tepozteco, Morelos, Mexico**

Day –1			Day +1			Day +2			Day +3			Day +4			Day +5		
Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%
–24	1.7	15.8	0	3.9	15.6	24	3.0	18.4	48	2.6	22.4	72	8.4	15.6	96	6.0	14.0
–24	3.2	17.0	2	2.2	22.8	26	7.0	14.8	48	10.9	11.0	74	5.5	9.0	96	3.5	10.6
–22	0.0	0.0	4	3.2	24.8	28	3.6	21.2	50	12.2	9.6	74	0.6	34.0	98	2.2	26.8
–22	1.2	21.2	4	3.6	15.4				50	9.5	11.2	76	5.6	14.4	98	2.2	31.8
–20	0.0	0.0	6	4.7	8.2				52	6.1	15.4	76	7.3	9.8	100	1.6	34.0
–20	0.4	22.8	6	3.9	17.4				52	6.4	15.2	78	7.7	12.8	100	1.2	34.0
–18	0.0	0.0	8	1.6	23.6				54	5.3	13.4	78	6.1	22.0	102	3.6	28.2
–18	1.8	21.0	8	4.9	17.4				56	4.9	15.4	80	6.4	13.8	102	7.8	16.0
–16	0.0	0.0	10	5.2	14.2				56	1.6	18.8	80	9.2	10.6	104	1.8	38.6
–14	0.6	17.4	10	4.0	15.0				58	6.4	15.2	82	11.4	1.6	104	13.4	12.0
–12	0.0	0.0	12	2.7	14.8				58	4.3	29.4	82	6.8	16.2	106	10.8	15.0
–12	1.0	33.0	12	2.5	20.2				60	7.7	10.2	84	9.2	7.2	106	1.6	26.0
									60	5.7	14.8	84	7.7	12.4	108	5.6	17.2
															108	5.1	15.0
x̄ =	0.8	12.4		3.5	17.5		4.5	18.1		6.4	15.5		7.1	13.8		4.7	22.8

APPENDIX 2. Continued.

***M. verbenaceus* (5924)—Grand Canyon, AZ**																							
Day –1			Day +1			Day +2			Day +3			Day +4			Day +5			Day +6			Day +7		
Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%	Age	Vol.	%
–18	10.0	13.2	0	32.1	15.4	24	50.8	16.0	48	47.9	16.0	72	55.2	18.8	96	76.4	19.4	120	61.7	20.1	144	76.6	15.8
–18	5.6	13.2	2	38.2	17.8	26	30.3	13.8	50	47.7	17.8	74	60.0	18.8	98	67.9	19.4	122	17.8	25.0	146	37.8	24.6
–16	23.9	14.0	4	27.9	15.6	26	26.2	15.8	52	51.3	18.6	74	41.0	16.8	98	60.0	19.2	124	23.9	15.2	148	13.9	25.2
–16	5.5	13.4	6	19.5	14.0	28	45.7	14.8	54	42.2	16.8	76	57.9	18.2	100	21.3	15.4	126	60.4	16.6			
–14	5.2	14.8	8	64.5	17.4	28	38.3	16.2	56	59.0	18.6	76	63.6	17.0	102	35.6	20.4	128	56.1	19.0			
–14	6.6	14.4	10	15.7	18.0	30	44.9	16.2	58	43.0	18.2	78	60.0	17.8	102	72.1	16.8	130	60.0	16.8			
–12	12.7	15.6	10	26.1	16.8	30	35.5	17.0	60	50.0	19.2	78	69.7	17.8	104	40.6	17.0	130	61.3	18.6			
–12	22.2	15.2	12	35.7	16.4	32	38.8	17.4	60	54.7	18.8	80	40.0	19.0	104	43.2	15.8	132	61.8	18.2			
			12	22.9	17.8	32	37.9	15.4				80	18.8	15.0	106	70.8	17.2						
						34	25.3	18.6				82	67.8	17.8	106	70.0	19.6						
						34	40.9	16.8				82	48.3	19.4	108	57.9	20.2						
						36	36.2	17.4				84	43.5	20.8	108	81.4	17.6						
						36	37.5	17.8				84	34.8	21.2									
$\bar{x}$ =	11.5	14.2		31.4	16.6		37.6	16.4		49.5	17.9		50.8	18.3		58.1	18.2		50.4	18.7		42.8	21.9

APPENDIX 3. Nectar production in flowers of greenhouse-grown plants under repeated sampling every 2 h versus only one sampling at 1600 h.

	0800		1000		1200		1400		1600		Totals		1600 only	
Population	μl	%	μl	%	μl	%	μl	%	μl	%	Σ, μl	%, x	μl	%
7113-19	9.5	13.5	7.0	12.0	0.2	3.8	1.0	12.0	0.1	14.0	17.8	11.0	4.0	21.3
7113-19	8.0	16.4	3.5	11.2	8.0	14.4	1.5	13.8	0.3	4.0	21.3	12.0	8.0	17.5
7113-19	2.0	18.0	1.0	10.0	1.5	16.0	3.0	18.0	9.6	17.1	17.1	15.8	3.0	25.4
7113-20	2.5	19.8	6.5	19.1	9.2	16.5	3.5	15.2	0.4	15.0	22.1	17.1	9.0	20.0
7113-20	1.2	13.6	3.5	13.0	4.0	14.0	2.8	15.0	0.1	7.0	11.6	12.5	9.2	24.3
7113-31	2.0	14.6	0.3	5.3	1.5	13.0	4.4	23.3	1.0	10.7	9.2	11.1	4.0	18.2
$\bar{x}$ =	4.2	16.0	3.6	11.7	4.1	13.0	2.7	16.2	1.9	11.3	16.5	13.2	6.2	21.1
7120-25	4.8	14.8	4.0	13.0	3.0	12.6	6.0	11.3	2.7	12.2	20.5	12.8	9.0	17.0
7120-25	3.5	18.6	9.0	18.2	5.0	15.6	9.5	13.7	4.5	12.3	31.5	15.7	10.2	16.1
7120-25	1.0	11.0	2.6	12.3	1.5	11.0	0.7	14.0	1.2	10.2	7.0	11.7	8.0	14.8
7120-28	2.0	17.7	0.6	11.2	5.0	15.1	5.0	16.4	2.6	15.0	15.2	15.0	9.0	16.2
7120-24	9.6	18.4	8.0	16.4	9.5	16.0	0.5	12.3	0.3	2.6	27.9	13.1	9.0	18.1
7120-28	8.8	14.5	2.0	9.0	2.5	12.0	2.5	13.1	4.0	12.0	19.8	12.1	4.5	15.0
$\bar{x}$ =	4.9	15.8	4.3	13.3	4.4	13.7	4.0	13.4	2.5	10.7	20.3	13.4	8.3	16.2
6651-9	10.0	13.0	8.0	10.6	3.0	7.4	1.0	13.8	1.0	13.4	23.0	11.6	0.2	7.0
6651-11	9.0	17.5	10.0	16.6	8.0	17.0	9.8	16.0	2.5	14.5	39.3	16.3	9.5	14.6
6651-15	1.0	23.4	1.0	20.6	1.5	20.4	4.0	17.5	9.5	17.0	17.0	19.8	9.2	20.3
6651-21	9.0	15.8	11.5	15.2	7.0	14.0	10.8	15.0	0.5	12.0	38.8	14.4	6.5	16.0
6651-21	8.0	15.9	4.0	14.5	8.6	13.4	3.0	13.6	9.0	16.0	32.6	14.7	4.5	15.7
6651-10	2.5	12.7	2.5	12.7	3.0	11.0	1.2	12.8	0.3	13.0	9.5	12.4	8.0	16.2
$\bar{x}$ =	6.6	16.4	6.1	15.0	5.2	13.9	5.0	14.8	3.8	14.3	26.7	14.8	6.3	14.9
6079-23	2.5	6.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	1.3	6.0	6.0
6079-10	0.4	26.0	0.7	23.6	0.8	18.5	0.0	0.0	0.0	0.0	1.9	13.6	8.5	13.6
6079-10	2.0	9.0	2.0	8.7	1.5	9.4	1.0	9.8	0.0	0.0	6.5	7.4	1.1	26.0
6079-23	0.0	0.0	0.7	12.7	2.5	17.6	3.5	14.1	1.0	13.0	7.7	11.5	3.0	11.4
6079-10	9.5	6.1	4.0	5.2	0.1	7.0	0.0	0.0	0.0	0.0	13.6	3.6	8.2	7.2
6079-21	0.5	8.1	7.5	7.5	3.0	7.0	0.9	9.3	1.0	8.0	12.9	8.0	4.0	12.0
$\bar{x}$ =	2.5	9.3	2.5	9.6	1.3	9.9	0.9	5.5	0.3	3.5	7.5	7.5	5.1	12.7
6103-130	1.0	34.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	6.8	0.0	0.0
6103-186	0.5	34.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.8	0.3	6.3
6103-130	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.3	0.0	0.0
6103-130	0.0	0.0	0.0	0.0	0.0	0.0	0.7	31.0	0.0	0.0	0.7	0.3	0.0	0.0
6103-119	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6103-186	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
$\bar{x}$ =	0.2	11.3	0.0	0.0	0.0	0.0	0.1	5.1	0.0	0.0	0.3	2.3	0.1	1.0
5875-246	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5875-239	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5875-246	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	34.0	0.2	6.8	0.0	0.0
5875-263	0.1	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.2	34.0
5875-262	0.4	34.0	2.0	11.7	0.0	0.0	0.0	0.0	0.1	8.0	2.5	10.7	0.0	0.0
5875-202	0.0	0.0	0.0	0.0	0.1	1.0	0.1	7.0	0.0	0.0	0.2	1.6	0.1	13.0
$\bar{x}$ =	0.1	6.1	0.3	2.0	0.0	0.1	0.0	1.1	0.1	7.0	0.3	3.2	0.1	7.8
6271-25	6.0	18.4	8.0	17.0	5.0	16.0	2.0	15.0	4.0	15.1	25.0	16.3	9.3	16.4
6271-8	10.8	15.5	4.5	15.4	9.0	14.3	11.5	13.2	9.3	12.0	45.1	14.0	8.5	15.3
6271-10	7.5	13.8	9.2	13.0	10.0	13.0	5.0	13.5	1.0	10.4	32.7	12.7	0.1	0.0
6271-28	2.5	16.8	0.5	17.0	3.5	16.3	0.7	7.0	1.2	14.3	8.4	14.3	7.0	9.6
6271-31	7.0	19.0	2.2	15.0	2.0	13.1	2.0	12.6	0.8	11.8	14.0	14.3	5.0	11.0
6271-28	8.2	17.0	13.0	15.6	9.7	14.0	7.0	12.6	1.8	12.5	39.7	7.9	9.4	14.2
$\bar{x}$ =	7.0	16.8	6.2	15.5	6.5	14.5	4.7	12.3	3.0	12.7	27.5	13.2	6.5	11.1

APPENDIX 3. Continued.

	0800		1000		1200		1400		1600		Totals		1600 only	
Population	µl	%	µl	%	µl	%	µl	%	µl	%	Σ, µl	%, x	µl	%
9102-17	0.0	0.0	4.0	14.0	0.2	34.0	0.0	0.0	1.4	12.5	5.7	12.1	2.0	19.3
9102-31	1.0	19.0	1.6	15.8	1.2	14.3	2.7	12.8	0.0	0.0	6.5	12.4	1.3	19.0
9102-11	0.5	29.4	0.2	34.0	0.0	0.0	0.9	17.7	0.0	0.0	1.6	16.2	1.1	21.2
9102-29	0.0	0.0	1.0	14.2	0.9	10.2	1.2	13.3	2.0	10.3	5.1	9.6	4.6	10.4
9102-8	3.0	14.3	0.1	7.0	0.1	1.0	0.2	0.0	0.1	1.0	3.5	4.6	1.2	13.9
9102-21	0.0	0.0	0.3	23.0	1.0	15.5	0.5	19.0	1.0	13.0	2.8	14.1	2.0	23.3
$\bar{x}$ =	0.7	10.4	1.2	18.0	0.5	12.5	0.9	10.4	0.7	6.1	4.2	11.5	2.0	17.8
5924-10	6.0	18.0	8.5	18.5	1.0	31.0	0.0	0.0	0.0	0.0	15.5	11.2	8.5	17.0
5924-22	9.5	17.2	3.7	16.6	8.0	16.3	5.0	13.2	10.0	16.1	36.2	15.9	3.0	19.2
5924-10	6.0	16.0	0.3	12.3	3.5	17.0	2.5	16.0	1.1	17.0	13.4	15.6	4.5	17.3
5924-10	6.0	15.2	1.4	12.0	2.0	14.2	1.0	10.5	0.0	0.0	10.4	10.4	1.2	19.0
5924-12	8.0	4.0	8.5	3.0	0.0	0.0	0.0	0.0	0.5	10.0	17.0	3.4	5.6	14.0
5924-35	3.5	12.4	1.5	12.0	4.0	6.8	1.2	7.3	4.0	5.4	14.2	8.8	5.2	14.2
$\bar{x}$ =	6.5	13.8	4.0	12.4	3.1	14.2	1.6	7.8	2.6	8.1	17.8	10.9	4.7	16.8

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NESTING AND SUMMER HABITAT USE BY TRANSLOCATED SAGE GROUSE (*CENTROCERCUS UROPHASIANUS*) IN CENTRAL IDAHO

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ABSTRACT.—We translocated 196 Sage Grouse (*Centrocercus urophasianus*) into Sawtooth Valley, Idaho, during March–April 1986–87 to augment a small resident population. Forty-four grouse equipped with radio transmitters were monitored through spring and summer. Nest sites ($n = 6$) had greater ($P = .032$) horizontal cover than did independent random plots ($n = 7$). During summer, grouse used sites ($n = 50$) with taller live and dead shrub heights, greater shrub canopy cover, and more ground litter ($P < .009$) than were found on dependent random plots ($n = 50$) 50–300 m from use sites. Distance to edge and mountain big sagebrush (*Artemisia tridentata vaseyana*) density best separated use sites from independent random plots in logistic regression analysis and correctly classified 64% of the use sites and 78% of the independent random plots. Sage Grouse used sites that had narrower frequency distributions for many variables than did independent plots ($P < .04$), suggesting selection for uniform habitat.

Key words: Centrocercus urophasianus, *dispersal, habitat use, home range, Idaho, radio telemetry, Sage Grouse, translocation.*

Sage Grouse have been translocated in Montana (Thompson 1946), New Mexico (Allred 1946), Wyoming (Allred 1946, Patterson 1952), Oregon (Batterson and Morse 1948), British Columbia (Hamerstrom and Hamerstrom 1961), and Colorado (C. E. Braun personal communication). Despite numerous early translocation efforts, only one study documented survival of translocated Sage Grouse (Musil et al. 1993), and little is known about habitat use by translocated birds. All spring and summer habitat-use studies (e.g., Klebenow 1969, Oakleaf 1971, Petersen 1980, Schoenberg 1982, Dunn and Braun 1986) involved established Sage Grouse populations.

Historically, Sawtooth Valley in central Idaho supported a population of Sage Grouse (Autenrieth 1981). Prior to 1980, at least six leks were active, but annual surveys by U.S. Forest Service (USFS) and Idaho Department of Fish and Game personnel indicated the breeding population declined from 1981, when 26 birds were seen on two leks, to 1986, when only one lek was attended by one male (A. L. Burton, USFS, interdepartment report). Although causes of the population decline are unknown, rangeland inventories conducted during 1985 and 1986 suggested the available habitat should support Sage Grouse (A. L. Burton, USFS, interdepartment report).

The objective of this study was to document nesting and summer habitat use by Sage Grouse translocated into former range in central Idaho. We tested the hypotheses that habitat characteristics were similar between sites used by translocated grouse and random sites as well as between nest and random sites.

STUDY AREA

Sawtooth Valley is at the headwaters of the Salmon River in central Idaho (Tuhy 1981). The valley is approximately 30 km long, 3–5 km wide, and 1960–2250 m in elevation. It is flanked to the west by the Sawtooth Mountains (>3200 m) and to the east by the White Cloud Mountains (>3500 m). The periphery of Sawtooth Valley is composed of rolling glacial moraines with slopes >10°. The valley floor is composed of glacial and alluvial deposits with slopes 0–5° (Tuhy 1981).

Average annual precipitation is 26 cm and average annual temperature is 6.5° C. The valley averages 2.5 m of snow, which accounts for 85% of the annual precipitation (Tuhy 1981). Sagebrush cover dominates approximately 125 km^2 (75%) of Sawtooth Valley. Mountain big sagebrush/Idaho fescue (*Festuca idahoensis*) is the major habitat type (Tuhy 1981).

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Wet meadows and riparian areas cover 19 km^2 (11%) of the valley, irrigated pastures 19 km^2 (11%), and isolated stands of lodgepole pine (*Pinus contorta*) 3 km^2 (2%; Musil 1989).

METHODS

During late March and early April 1986 and 1987, we captured 196 Sage Grouse (46 adult females, 19 yearling females, 115 adult males, 16 yearling males) by spotlight trapping (Giesen et al. 1982) on 11 leks from nonmigratory populations (J. W. Connelly personal observation) in southeastern Idaho. Capture areas were at similar elevations approximately 144 km from Sawtooth Valley. Grouse were classified to age and sex (Dalke et al. 1963) and leg-banded at the capture site. Males were transported in wooden crates and females were moved individually in modified cardboard boxes to reduce head-scalping and other injuries (Patterson 1952). Birds were transported by truck to Sawtooth Valley each morning after capture and moved by snowmobiles to the release site adjacent to the last active lek. Releases occurred from 19 March to 6 April 1986 and 25 March to 1 April 1987.

We equipped 44 (22%) grouse (31 females, 13 males) with solar-powered radio-transmitters (Musil 1989, Musil et al. 1993) attached to ponchos (Amstrup 1980). Fifteen grouse (8 females, 7 males) were marked with radios in 1986 and 29 (18 females, 11 males) in 1987. Weight of telemetry packages (<25 g) was <2.2% of the mean body weight of female grouse.

We located birds at least twice per week, equally dividing locations during the day among three periods (Dunn and Braun 1986). We tracked radio-marked birds from the ground using a hand-held 4-element Yagi antenna and receiver (Mech 1983).

Radio-locations were obtained by walking a 15–30-m-radius circle around the signal (Musil et al. 1993). We plotted radio-locations on aerial photographs and 7.5-minute U.S. Geological Survey orthoquadrangle topographic maps overlaid with the Universal Transverse Mercator (UTM) grid system (Lancia 1974) scaled to 100 m^2/grid.

Habitat Characteristics

NEST SITES.—Nests of translocated Sage Grouse were located by telemetry and incidental sighting. Nest site characteristics were measured after nesting efforts ceased. At each nest the number of shrubs in contact with the nest bowl was counted. Height of the shrub over the bowl and area (length × width) of the shrub mass surrounding the nest were measured. Density of shrubs ≤40 cm and >40 cm tall was measured within a 2-m radius of the nest. A cover board (Jones 1968) was placed in the nest, and horizontal cover was estimated at 2 m from the nest at 0° and 45°. The board was also placed flat in the nest and cover at 90° was measured. Four 20-m transects were positioned at cardinal directions intersecting the nest, and shrub cover was measured using the line-intercept method (Canfield 1941). Shrub and grass heights were measured at 5-m intervals along the transects.

To determine whether Sage Grouse were selecting nest sites based on stand characteristics, we established a dependent random plot in 1987 at a random direction and distance 50–300 m from each nest site. A corresponding independent random plot was located by randomly selecting two 5-digit numbers corresponding to the last five numbers of the east and north UTM coordinates covering the study area (167 km^2). To find the independent random plot, we paced the distance along a compass line from the nearest landmark to the point. Only points in sagebrush habitat were used for independent random plots because this is the only habitat used for nesting by this species (Patterson 1952, Petersen 1980, Wakkinen 1990, Connelly et al. 1991).

DAILY USE SITES.—Vegetative and topographic variables were measured at sites used by radio-marked Sage Grouse during May–July 1987. Use plots were centered at radio-locations and selected uniformly among daily use patterns of Sage Grouse (Dunn and Braun 1986). Habitat characteristics were also measured at dependent and independent random plots as described for nest sites.

At each use site we measured vegetation along two parallel 15-m transects placed 8 m apart. Transects were positioned perpendicular to the contour of the slope and centered within a 60-m-radius circle for use sites. Shrub canopy cover was measured by line-intercept (Canfield 1941). Shrub density (plants/m^2) within 0.5 m of each side of the transect was measured, and a clinometer was used to record slope at each vegetation site.

We estimated understory cover with modified Daubenmire (1959) 4 × 5-dm plots at 1.5-m intervals (20 frames/site) along the transects (Mosley et al. 1986). At each Daubenmire plot, heights of the closest live and dead shrub <1 m from the transect were measured.

Locations of vegetation sampling sites were plotted on 7.5-minute orthoquadrangle topographic maps, elevations recorded, and the distance to the nearest change in cover type (i.e., pasture, riparian, wet meadow, or timber) measured with an electronic planimeter.

VEGETATION ANALYSIS.—Depending on normality, univariate parametric or nonparametric statistical tests were used for comparing equality of both means and variances between use and random sites. Separate analyses were conducted for use vs. dependent random sites (matched pairs) and between use and independent random sites using SAS (SAS Institute, Inc. 1985) and Statistix II (Analytical Software, Box 130204, St. Paul, Minnesota 55113) computer programs.

We used logistic regression (Harrell 1985) to identify variables that best distinguished Sage Grouse use from independent random sites. Maximum-likelihood estimates were computed to determine coefficients for variables in the predictive model. The significance level to enter and stay in the logistic regression model was set at .10, and addition of variables to the model was stopped once the X^2 test of the residual variables was no longer significant.

Nonparametric tests were used to compare nests with random plots because of the small sample of nests (n = 6). Wilcoxon's signed rank test (Conover 1980) was used to compare height of the shrub covering the nest and average height of live shrubs along the transects surrounding the nest.

We did not intentionally flush radio-marked grouse; thus flock composition was largely unknown. Occasionally, mixed-sex flocks were flushed, which suggested that plots used for habitat sampling were not represented by one sex. Therefore, we did not compare habitat use by male and female grouse.

RESULTS

Nest Sites

At least one translocated Sage Grouse nested in 1986 and six nested in 1987. Two of the grouse that nested in 1987 were birds released in 1986; the others were released during spring 1987. Vegetation at nest sites (n = 6) did not differ (P > .10) from dependent random plots (Wilcoxon signed rank test, $P \geq .249$ for all values). Although average height of shrubs covering nests ($\bar{x}$ = 50.7 ± 6.7 cm) was greater (P = .04) than average shrub height surrounding nests ($\bar{x}$ = 27.3 ± 4.0), there were no differences in shrub height or cover at nest sites compared with dependent or independent random sites. Grouse nested at sites with greater (P = .03) horizontal cover at a 45° angle to the nest ($\bar{x}$ = 86.0 ± 12.5) than at independent random sites ($\bar{x}$ = 66.9 ± 16.5).

Daily Use Sites

Between 22 May and 23 July 1987, 50 use sites were sampled for 15 (3 males, 12 females) radio-marked grouse, with an equal number of dependent and independent random sites. Dependent random sites averaged 163 ± 16 m from use sites. Grouse used sites with more shrub canopy cover ($P \leq .01$), greater litter cover ($P \leq .01$), and taller live and dead shrubs (P = .00) than at dependent random sites (Table 1). Variance tests indicated few differences in frequency distributions between Sage Grouse use and dependent random sites (Table 1).

Sage Grouse used areas with flatter slopes (P < .01), farther from habitat edges (P = .01), with more litter cover (P = .00), less bare ground (P = .00), and greater density of mountain big sagebrush (P = .04) (Table 1) than at independent sites. Variance tests indicated that grouse used narrower frequency distributions of slope, elevation, live shrub canopy cover, bare ground, density of shrubs other than sagebrush, and live shrub height (P = .00) but wider distributions of distances to edge (P = .00), dead shrub canopy cover (P < .01), total shrub density (P = .03), and dead shrub height (P = .00) (Table 1).

Two variables were identified by logistic regression to best separate use sites from independent random sites. Distance from edge and mountain big sagebrush density correctly classified 64% of the use sites and 78% of the independent random sites. The probability that a site would be classed as a use site increased as distance from habitat edge and density of mountain big sagebrush increased.

TABLE 1. Habitat characteristics at translocated Sage Grouse use sites, dependent random and independent random sites in Sawtooth Valley, Idaho, 1987.

	Grouse ($n = 50$)		Dependent ($n = 50$)		P		Independent ($n = 50$)		P	
Habitat variable	$\bar{x}$	SD	$\bar{x}$	SD	H_o: equal means[a]	H_o: equal variances	$\bar{x}$	SD	H_o: equal means[a]	H_o: equal variances[b]
Slope (°)	3.4	4.8	2.9	4.4	.66	.00	7.6	8.7	.01	.00
Elevation (m)	2141	37	2139	37	.59	.59	2148	78	.49	.00
Edge distance (m)	392	283	400	271	.63	.77	225	172	.01	.00
Canopy cover (%)										
Mtn. big sage[c]	17.6	6.0	14.9	7.0	.01	.27	16.0	11.0	.19	.00
All sagebrush	17.9	6.3	14.9	7.0	.01	.47	16.7	10.5	.48	.00
Other shrubs	0.7	1.9	0.4	1.4	.15	.00	2.1	5.6	.48	.00
Dead shrubs	4.8	4.5	4.7	4.3	.82	.78	4.2	3.7	.93	.01
Live shrubs	18.5	6.7	15.3	7.3	.01	.50	18.8	11.6	.91	.00
All shrubs	23.3	6.9	20.0	7.5	.00	.53	23.0	11.6	.86	.00
Groundcover (%)										
Forbs	4.9	4.8	4.1	2.5	.69	.06	4.2	4.2	.29	.72
Grass	26.1	10.3	26.2	11.4	.97	.49	23.8	12.3	.30	.22
Litter	29.0	9.7	25.3	10.5	.01	.56	21.3	11.7	.00	.01
Bare ground	31.0	14.0	34.9	14.2	.06	.92	43.7	21.0	.00	.01
Shrub density (plants/m^2)										
Mtn. big sage[c]	1.61	0.68	1.57	0.76	.70	.44	1.28	0.62	.04	.69
All sagebrush	1.66	0.75	1.57	0.76	.48	.98	1.43	0.69	.24	.69
Other shrubs	0.13	0.32	0.12	0.37	.40	.00	0.19	0.42	.32	.00
Dead shrubs	0.68	0.57	0.68	0.58	.95	.92	0.60	0.47	.76	.02
Live shrubs	1.75	0.81	1.69	0.88	.63	.58	1.62	0.75	.71	.52
All shrubs	2.47	1.00	2.37	0.92	.35	.55	2.22	0.73	.16	.03
Shrub height (cm)										
Live	36.3	6.7	31.5	6.2	.00	.59	34.5	11.4	.34	.00
Dead	18.0	9.6	15.5	8.5	<.00	.10	25.8	7.0	.16	.00

[a] Paired *t* test or Wilcoxon signed rank test depending on normality and equality of variances.

[b] *F* test or squared ranks test depending on normality.

[c] Mountain big sagebrush.

DISCUSSION

Nest Sites

All nests were under sagebrush, similar to findings for many established populations (Patterson 1952, Klebenow 1969, Wallestad and Pyrah 1974, and Petersen 1980) but somewhat different from Sage Grouse nesting in southeastern Idaho (Connelly et al. 1991). No differences were detected between nest sites and dependent plots in the same stand of sagebrush, but hens did nest under shrubs that were taller than shrubs surrounding the nest. These findings are similar to those reported by Wallestad and Pyrah (1974) and Petersen (1980) for established populations. However, Wakkinen (1990) reported that Sage Grouse in southeastern Idaho nested under taller shrubs with a larger area than shrubs in the same stand. Hens may select tall plants and clumps of shrubs for nest sites because these provide more visual obstruction to predators.

We detected few differences in vegetation between nest sites and independent random sites. Wakkinen (1990) reported similar findings and suggested this indicated an abundance of suitable nesting habitat.

Daily Use Sites

Translocated Sage Grouse in Sawtooth Valley used sites with greater physical obstruction than at dependent random sites, and these may have provided more concealment from predators. Grouse use sites also had greater litter cover, which may be related to shrub cover and live shrub height as well as insect abundance (Patterson 1952, Johnson and Boyce 1990).

In a comparison of summer use sites with independent random plots, grouse used flatter sites near the center of the valley rather than the rolling glacial moraines along the perimeter. The central part of the valley has extensive stands of mountain big sagebrush, whereas mixtures of sagebrush and antelope bitterbrush (*Purshia tridentata*) occur on the moraines. Areas used by grouse had little interspersion of habitat edges when compared to sagebrush along the perimeter of the valley. The perimeter had narrow peninsulas of sagebrush on steeper slopes that extended into lodgepole pine timber. These sites were not used by radio-marked Sage Grouse.

Ratti et al. (1984:1193) tested variances between Spruce Grouse (*Dendragapus canadensis*) use sites and random plots and stated that "these differences indicated a preference for sites having habitat characteristics with less variation than the general environment." Similarly, translocated Sage Grouse used narrower ranges for several microhabitat characteristics, both topographic and structural, compared with habitat available throughout the study site. However, within a stand of sagebrush, translocated grouse selected habitat with greater-than-average values rather than narrower frequency distributions.

Translocated Sage Grouse were not associated with edges of cover types as was reported for grouse in Colorado (Dunn and Braun 1986). Grouse in Sawtooth Valley were associated with greater-than-average structural characteristics of sagebrush within a stand (i.e., taller brush and greater canopy cover). This suggests that variability in habitat structure not only among but also within stands of sagebrush is important to Sage Grouse by providing adequate habitat during different seasons and for diurnal uses (Dunn and Braun 1986).

Characteristics of nesting and summer habitats used by translocated grouse within Sawtooth Valley were generally similar to those reported for established Sage Grouse populations in many parts of the species' range. This similarity suggests that translocations of Sage Grouse, if carefully planned, are a feasible method of augmenting or reestablishing Sage Grouse populations (Musil et al. 1993). Patterson (1952) concluded that restoration of relatively small Sage Grouse populations by translocation was not effective because of the birds' tendency to disperse from the release site. Contrary to Patterson's (1952) findings, Sage Grouse translocated into the Sawtooth Valley remained near the release site (Musil et al. 1993). Dispersal of these birds may have been greatly reduced because they were released during the breeding season, into the relatively insular and isolated Sawtooth Valley, and, perhaps most importantly, into an area with adequate spring and summer habitat.

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VEGETATION ZONES AND SOIL CHARACTERISTICS IN VERNAL POOLS IN THE CHANNELED SCABLAND OF EASTERN WASHINGTON

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and Benjamin A. Zamora[3]

ABSTRACT.—Vernal pools are seasonal pools occurring in Mediterranean-type climates within which grow concentric zones of vegetation. We studied two vernal pools that lie within an *Artemisia tridentata/Festuca idahoensis* shrub-steppe landscape in the Channeled Scabland of eastern Washington to determine the relationship between vegetation zonation and soil characteristics. Abundant plant species in the pools include *Elymus cinereus, Poa scabrella, Lomatium grayi, Allium geyeri, Eleocharis palustris, Epilobium minutum, Myosurus aristatis, Deschampsia danthonioides*, and *Psilocarphus oregonus*. We surveyed topography, measured plant species frequency and cover to describe the vegetation zones, and used Sorenson's index of percent similarity to verify our designation of plant zones as communities. In one pool we described soil profiles and sampled soils throughout the growing season according to plant communities. We analyzed soils for pH; electrical conductivity; sodium, calcium, and magnesium ions; sodium adsorption ratio; particle size; organic carbon; and water matric potential. ANOVA tests of soil characteristics and topography among plant communities showed that only differences in topography are statistically significant. There are, however, trends in particle size, some soil chemical parameters, and soil moisture potential among plant communities along the topographic gradient. Electrical conductivity decreased with increasing dryness of the soil through the spring and summer. Seasonal changes in soil moisture potential showed that shallower soils in the centers of pools are wetter during the wet season and drier during the dry season than are deeper soils. These changes in moisture may be the most important influence on vegetation distribution within the vernal pools.

Key words: vernal pool, vegetation zones, soil characteristics, eastern Washington.

Vernal pools occur in grasslands, parklands, and forests where Mediterranean-type rainfall patterns prevail. These biotic systems are geographically widespread and are among the casualties of the widespread modification of natural landscapes. Vernal pools are typically formed in shallow depressions where soils have impermeable hardpans or are underlain by impermeable bedrock. Vernal pools fill with water from winter rains (and snowmelt in colder climates) and gradually dry during late spring and early summer through evapotranspiration. Vegetation within the pools is different from that of the surrounding landscape and often forms a pattern of more or less concentric zones of different species groupings. These unique natural sites are excellent for studying ecological processes in relatively self-contained ecosystems.

Zonal vegetation patterns of vernal pools have attracted many researchers in California, where vernal pools are numerous. Scientists have approached the study of pools by examining aspects of seasonal hydrology and soil physical and chemical characteristics. One theory is that seasonal duration of standing water directly affects distribution of plant species according to their ability to germinate and/or grow either under water or within the shortened growing season after evaporation of the pool (Purer 1939, Lin 1970, Zedler 1987). Other researchers have found trends in soil particle size, available nitrogen and phosphorus, exchangeable magnesium and sodium, electrical conductivity, pH, and unsaturated soil moisture potential that correlate to position along the gradient from outside to inside the pool (Lathrop 1976, Bauder 1987). Thus, a second theory is that soil chemical and physical factors influence plant distribution.

Researchers have taken different views as to whether there are spatially discrete zones of species groupings (plant communities) or whether the distribution of species is continuously variable, with overlapping growth ranges. Some argue the latter case and maintain that only temporal groupings of species occur (Purer 1939, Zedler 1987). The alternate view has been supported by several studies whose authors typically have delineated three to five zones, one of which is the surrounding grassland vegetation (Lin 1970, Kopecko and Lathrop 1975, Macdonald 1976).

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Pools of the Pacific Northwest, specifically those in central and eastern Oregon and Washington, have been little studied. We chose two vernal pools in eastern Washington to examine the validity of vegetation zonation and to determine a possible relationship between vegetation zones and soil properties.

STUDY AREA

We chose to study vernal pools in the Marcellus Shrub Steppe Natural Area Preserve (47°14′N, 118°24′E, Sec. 15, T20N, R35E, WBM, in Adams County, Washington) because the site has not been seriously degraded by past grazing (Schuller 1984) and because it has been fenced as a preserve since 1986. The preserve covers approximately 290 ha (Fig. 1) and is at the northeast end of a larger tract of uncultivated scabland, surrounded by wheat fields, that extends west-southwest for approximately 6.5 km along Rocky Coulee, part of the Channeled Scabland, an enormous landscape in eastern Washington formed by repeated cataclysmic glacial outburst floods during the Pleistocene (Fig. 1; Baker 1978).

Surrounding the Channeled Scabland and in some areas within it are deposits of Pleistocene-age loess (windblown silt) many meters thick (Busacca 1991) that overlie the Miocene Columbia River Basalt. The last glacial floods about 15,000 years ago removed most of the older loess from the Telford–Crab Creek Scabland tract, including the project site, so that the thin cover of loess presently on the site has accumulated, and soils have developed, only since the last floods. Deeper soils of the site, approximately 40–150 cm deep, are on the loess mounds. Soils within the vernal pool basins are only approximately 10–30 cm deep. Most vernal pools are part of an interrupted channel system running through the study site (Fig. 1). Solitary pools and those in the intermittent channel system may have been formed by a combination of cataclysmic flood scour, variable loess deposition, and local slope erosion.

Rainfall distribution of the Columbia Plateau is a Mediterranean type. Forty years of average temperatures, precipitation, and evapotranspiration were used to produce a climate diagram (Thornthwaite 1948, NOAA 1988–89), which indicated that November through March are the months of greatest precipitation (approximately 60% of the yearly total) and soil water storage, whereas April through October bring little precipitation and high evapotranspiration.

METHODS

Average monthly precipitation and temperature values recorded at the Ritzville 1SE weather station (NOAA 1988–89) were used to compute average monthly evapotranspiration for the months of pool filling and plant growth in the study year (Palmer and Havens 1958). Precipitation values for November 1988 through March 1989, the months typically receiving the majority of precipitation, and April through June of 1989, the months during which most vernal pool species grow vegetatively and flower, were compared with average values for these time periods.

We chose two vernal pools for this study and called them South Pool and North Pool. South Pool is 109 m long and 70 m wide, and North Pool (Fig. 2) is 57 m long and 34 m wide. A 25-m-wide swath through South Pool (Fig. 3) and all of North Pool were surveyed using a Leitz Set2 Total Station Electronic Distance Meter and SDR22 data collector to produce topographic maps. Within the two pools, groups of plant species formed concentric zones from the outsides to the centers of the pools. Although zones were uneven in width and some were even absent in some places, the sequence in which they appeared was consistent. Six vegetation zones were identified in each pool. Boundaries of the vegetation zones were marked along transect lines across each pool. We marked four sites for plant and soil sampling within each vegetation zone, two on either side of each pool center (Fig. 3).

Vegetation (in both pools) and soils (in South Pool only) were sampled on 23 April, 10 May, 24 May, 11 June, 29 June, and 13 July 1989. Repeated sampling was done to monitor maturation of vegetation. When plants within each zone reached their seasonal maturity, we measured frequency and coverage for each

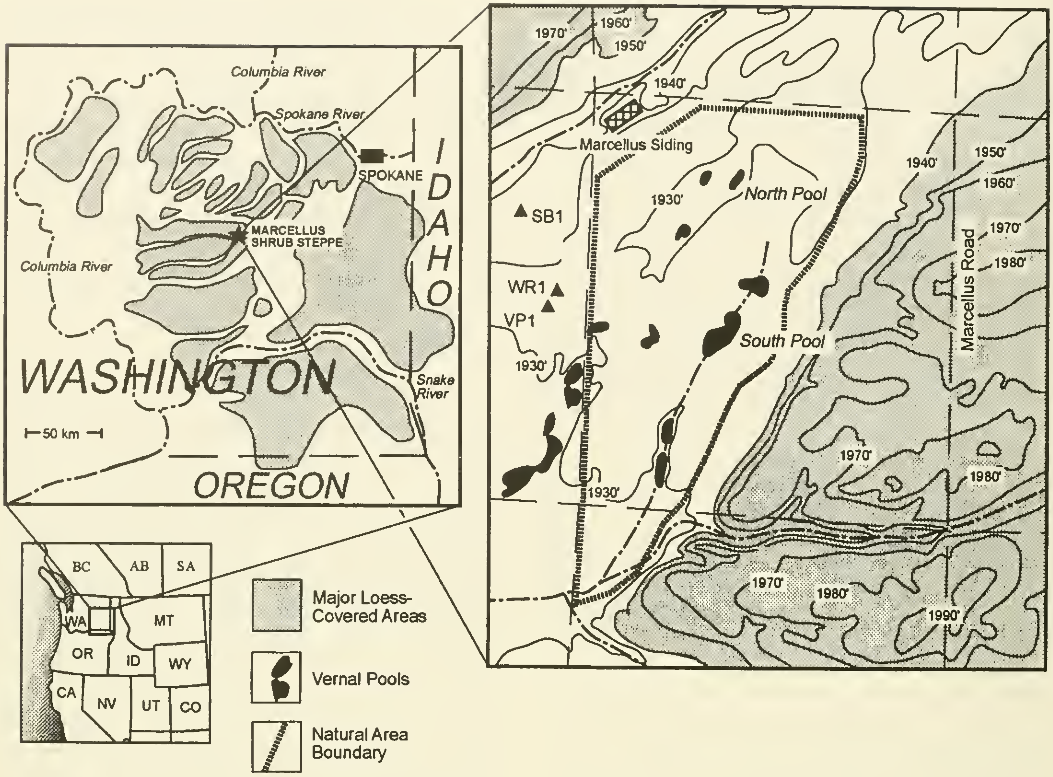
Columbia River
Spokane River
SPOKANE
IDAHO
MARCELLUS SHRUB STEPPE
Columbia River
WASHINGTON
Snake River
50 km
OREGON
BC
AB
SA
WA
MT
OR
ID
WY
CA
NV
UT
CO
Major Loess-Covered Areas
Vernal Pools
Natural Area Boundary
1970'
1960'
1950'
1940'
Marcellus Siding
SB1
1930'
North Pool
WR1
VP1
South Pool
1940'
1950'
1960'
1970'
1980'
Marcellus Road
1930'
1930'
1970'
1980'
1970'
1980'
1990'

Fig. 1. Map of the Marcellus Shrub Steppe Natural Area in eastern Washington state with inset map showing generalized topography, natural area boundary, and principal vernal pools. Triangles are locations of the sagebrush (SB1), wildrye (WR1), and vernal pool (VP1) soil profile sampling sites; North Pool and South Pool are labeled.

species in forty 20 × 50-cm plots along contours. We used nested frequency plot sizes of 5 × 5 cm, 12.5 × 20 cm, 20 × 25 cm, 20 × 37.5 cm, and 20 × 50 cm and cover classes of 0–5%, 5–25%, 25–50%, 50–75%, 75–95%, and 95–100% (Daubenmire 1970). Frequency and cover values were averaged over the forty plots for analysis.

Soil samples were collected in South Pool with a 2-cm-diameter probe. The first sets of soil samples were collected at site stakes. On each successive date, samples were taken approximately 10 cm from the previous sample at the same elevation as the site stake. Sampling depth increments were 2–10 cm, 10–30 cm, 30–60 cm, 60–90 cm, etc., until we reached basalt bedrock (0–2 cm consisted of ash from the 1980 eruption of Mount St. Helens).

We measured the matric potential of soil moisture in soil samples collected on all dates using the filter paper equilibration method (Campbell and Gee 1986, Campbell 1988). We produced a moisture characteristic curve specifically for the filter paper (Whatman #42) used for determination of water potential from water content. Organic carbon and particle-size distribution were measured using wet combustion (Nelson and Sommers 1975) and the hydrometer method (Gee and Bauder 1986), respectively. The only pretreatment used in the particle-size analysis was sodium hexametaphosphate. We analyzed the 2–10-cm samples collected on 24 May from sites S1–S12.

Saturation extracts (using distilled H_2O) were collected from all samples from the 23 April and 28 June sampling dates (early and late in the growing season in the pools) and from all morphological description site samples. Electrical conductivity (EC) and pH were measured on the extracts, as well as soluble Na^+, Ca^{+2}, and Mg^{+2} to determine the sodium adsorption ratio (SAR). All ion concentrations were measured on an atomic absorption spectrophotometer.

To observe morphological properties of the soils (e.g., thickness of horizons and presence

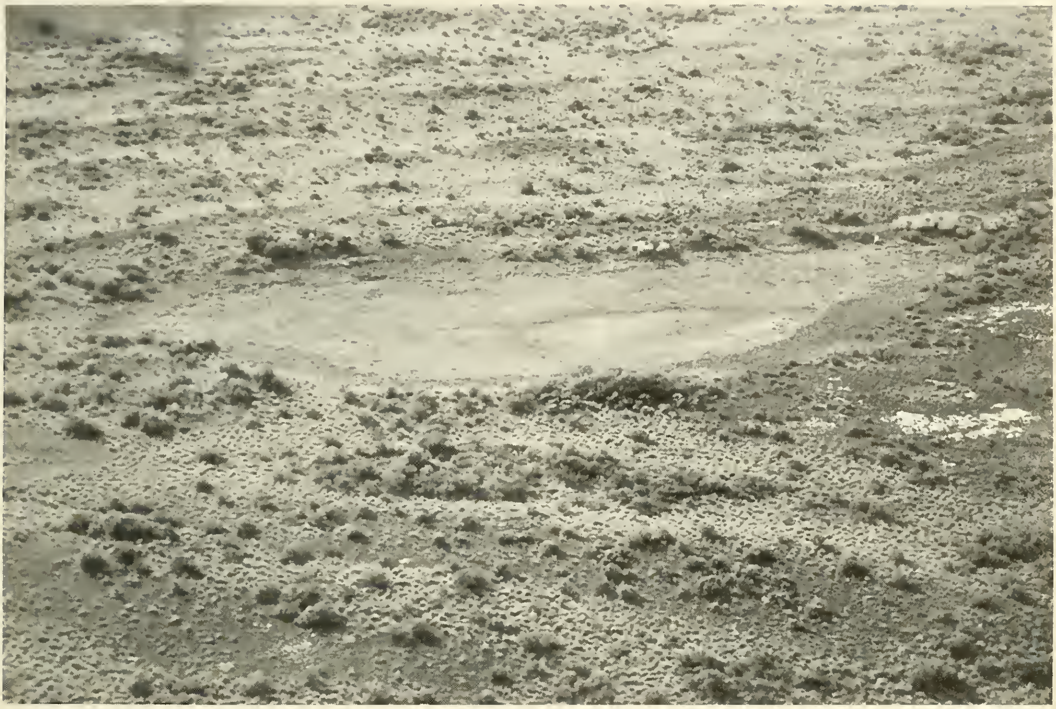

Fig. 2. Low-angle oblique aerial photograph of North Pool taken in May 1990. View is to the west; the pool is 57 m in length. *A. tridentata* is the dominant shrub in the plant zone 1 area surrounding the pool.

of structure that would indicate certain pedological processes), we excavated three soil pits: one in an upland position surrounding the pools (SB1), one in a pool rim (WR1), and one in a pool basin (VP1). To avoid damaging pools of the preserve, we located pits in the adjacent scabland tract (Sec. 16, T20N, R35E; Fig. 1), where soils were similar to those of the study site. Morphological features were described, block descriptions written, and horizons sampled for the three profiles. Block descriptions are in Crowe (1990). The three profiles were classified according to Keys to Soil Taxonomy (Soil Survey Staff 1990). We also analyzed horizons for particle size and SAR according to methods discussed above.

Vegetation, soil, and topographic data were analyzed using descriptive and inferential statistics. From the vegetation tallies we compared different vegetation zones (e.g., zone 1 vs. zone 2, zone 1 vs. zone 3, etc.) using Sorensen's similarity index for frequency (combining all frequency plot sizes) and for frequency weighted by cover (Barbour et al. 1980). Zonal elevations, particle-size classes, and organic matter were statistically compared among zones using a one-way analysis of variance (ANOVA). A repeated-measures ANOVA was used to analyze differences in soil matric potential among the vegetation zones over all five sample dates. The repeated-measures ANOVA was also used to analyze EC, pH, and SAR among all plant zones and between the 23 April and 28 June sampling dates.

RESULTS

Precipitation

Comparison of the long-term average monthly precipitation with monthly totals for November 1988 through March 1989 revealed that total precipitation for that period was almost identical to the long-term average (169 mm during 1988–89 vs. 168 mm on average). April through June precipitation totals (58 mm) were also quite similar to the long-term average (63 mm); however, only 1.52 mm of rain fell in June compared to an average of 23 mm, and temperature and evapotranspiration were slightly higher than average. Matric potential values measured during April and May thus were probably indicative of the moisture normally available to vernal pool species at that time of year, and those measured in June were

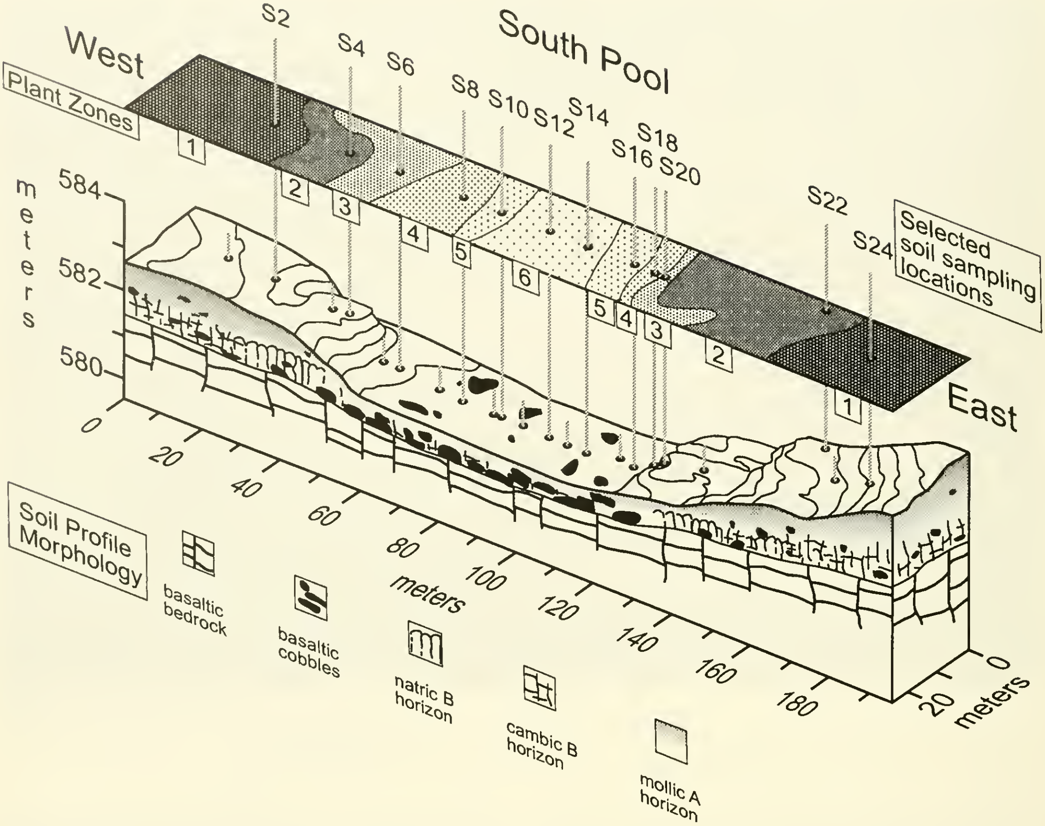
West
South Pool
East
Plant Zones
1
2
3
4
5
6
5
4
3
2
1
S2
S4
S6
S8
S10
S12
S14
S16
S18
S20
S22
S24
Selected soil sampling locations
meters
584
582
580
0
20
40
60
80
100
120
140
160
180
meters
0
20
meters
Soil Profile Morphology
basaltic bedrock
basaltic cobbles
natric B horizon
cambic B horizon
mollic A horizon

Fig. 3. Topographic cross section through South Pool showing selected soil sampling locations, plant zones, and soil profile morphology. Note ca 10X vertical exaggeration. Shaded areas indicate plant zones. Zones are numbered and correspond to text. S2–S24 are selected soil sampling locations.

probably lower than normal. The pools probably dried faster than they do in some years, which would shorten life cycles of annuals that normally flower during June or early July.

Vegetation

We identified six vegetation zones (zones 1 through 6) in South Pool (Fig. 3), five similar zones (zones 1, 3, 4, 5, and 6) in North Pool, and an additional zone (zone 7) of rush (*E. palustris*) that occurs only in North Pool. Total species cover and frequency in the 25% cover class for all zones in the South and North pools are shown in Table 1. Zone 1 was an example of a shrub-steppe community as described by Daubenmire (1970). It was dominated by *F. idahoensis* with a scattered shrub overstory of *A. tridentata*. More abundant forbs included *Plectricus macrocera*, *Plantago patagonica*, and *Draba verna*. Shrub height was about 70 cm and herb height about 40 cm. Zone 2 was dominated by *E. cinereus*, with a shrub overstory of *Chysothamnus nauseosus* and *C. vicidiflorus*. The more abundant forbs included *Senecio interrigemus*, *P. macrocera*, *D. verna*, and *Achillea millefolium*. Average height of vegetation in this community was about the same as in zone 1.

Zones 3–7 had no shrub overstory. In zone 3 *Poa scabrella* (40 cm in height) dominated, with *Lomatium grayi*, *A. geyeri*, and *Montia linearis* scattered throughout. *Deschampsia danthonioides* had very high cover in zones 4, 5, and 7. Other forbs and graminoids in zones 4 and 5 were *E. palustris*, *Agrostis diegoensis*, and *Agoseris heterophylla*. Forbs that distinguished zone 4 were *A. geyeri* and *E. minutum*; those that distinguished zone 5 were *Navarettia intertexta*, *Grindelia nana*, and *Myosuris aristatis*. Zone 7 had an abundance of *E. palustris* and well-distributed *M. aristatus*, *Alopechurus geniculatus*, and *E. minutum*. Vegetation height in these zones averaged 30 cm. Zone 6 was dominated by the low-growing annual forbs *N. intertexta* and *Plagiobothrys scouleri* (5–10 cm). Other forbs included *Psilocarphus oregonus* and *G. nana*.

We calculated similarity indices from our comparisons of plant communities of different zones within each of the two pools (Table 2). Results from comparisons using absolute frequency of species alone resulted in higher similarity indices between zones, whereas the addition of total canopy cover of species reduced most indices substantially. In the latter comparison only the comparison of zones 4 and 5 in South Pool and zones 5 and 7 in North Pool produced similarity indices greater than 50%.

Species that were fairly well established (i.e., they have high cover and/or frequency percentages) in two or more zones were mostly annual forbs and graminoids: *D. verna*, *A. heterophylla*, *E. minutum*, *D. danthonioides*, *A. diegoensis*, *N. intertexta*, and *M. aristatus*. In addition, three perennial herbs, *E. palustris*, *G. nana*, and *A. geyeri*, had a strong presence in more than one zone. Species that were noticeably unique to one zone were *F. idahoensis* and *A. tridentata* (zone 1), *E. cinereus* and *Chrysothamnus* spp. (zone 2), *P. scabrella* (zone 3), and *Boisduvalia stricta* (zone 6).

Soils

Microtopography, soil sampling points, and soil morphology are depicted for South Pool in Figure 3. An ANOVA of zonal elevation means demonstrated strongly significant differences among zones in each pool ($P < .0001$).

Soil profiles examined in the soil profile pits off the Marcellus site confirmed morphological characteristics of the soils surrounding (SB1), on the margins of (WR1), and within (VP1) vernal pools of the area, including those of North and South Pool (full soil profile descriptions in Crowe 1990). We produced a cross section showing the soil morphology of South Pool (Fig. 3) based on features seen in the offsite soil profile pits combined with soil properties and depths to bedrock measured during the repeated soil sampling of South Pool. SB1 was typical of the deeper soils in the shrub-steppe zone surrounding the pools. It is classified as a Xerollic Camborthid. VP1 was typical of the shallow, stony soils within the pools and is classified as a Lithic Camborthid. The two soils differed primarily in that VP1 was shallower to bedrock (33 cm in VP1, 116 cm in SB1). Neither of these soils had strongly developed soil profile features. They consisted principally of a dark, organic matter–rich mollic epipedon or topsoil horizon typical of steppe soils, and a blocky brown cambic subsoil horizon.

WR1 was typical of the pool rim or margin landscape position that supported the wildrye zone (zone 2) . It is classified as a Lithic Natrixeroll and is distinguished by its natric horizon (a clay-enriched or argillic horizon caused by a high exchangeable sodium percentage), shallow depth to bedrock, and mollic epipedon. The SAR (a measure of the dominance of sodium on the exchange complex of clay colloids) of the natric horizon of WR1 was 9.7, which is less than the value of 13, i.e., the lower limit set for the definition of the natric horizon (Soil Survey Staff 1990); however, other features typical of the influence of high exchangeable sodium were present, including columnar structure in the natric horizon, dark organic colloid stains on these columns, and an overlying eluvial horizon. Clay content of the natric horizon of WR1 was 17.0% compared to 11.0% in the overlying eluvial horizon.

ANOVAs performed on soil physical and chemical properties among zones were not statistically significant, but there are recognizable trends in some properties that may have ecological significance. Sand, silt, and clay contents differed with respect to South Pool topographic positions (Fig. 4). Sand percentage was greater and silt percentage was less in zone 3 than in other zones. In zone 3, at the bottom of the pool "rim," erosion and deposition may have caused a winnowing of fines from and an accumulation of sand in the soils. Clay content increased modestly from the outer zone to the center of South Pool. Organic carbon values were higher in the plant zones dominated by *A. tridentata*, *E. cinereus*, and *P. scabrella* (zones 1, 2, and 3) than in the remaining zones of South Pool (Fig. 4).

Soil-water matric potentials were similar, zone by zone, in the 2–10-cm and 10–30-cm depth increments on the first sampling date, 24 May (Fig. 5). On successive dates the 2–10-cm increment dried more than did the 10–30-cm increment as plants extracted soil moisture from the near-surface zone and soil moisture evaporated from the soil surface. On 11 June in

TABLE 1. All-species rélève showing total canopy cover and percent frequency in the 25% cover class by vegetation zone.

	% total cover / % frequency in 25% cover class										
Species	Zone 1 South	Zone 1 North	Zone 2 South only	Zone 3 South	Zone 3 North	Zone 4 South	Zone 4 North	Zone 5 South	Zone 5 North	Zone 6 South	Zone 6 North	Zone 7 North only
SHRUBS												
Artemesia tridentata	4.9/2.5	0.9/2.5										
Artemesia tripartita		3.3/2.5										
Chrysothamnus viscidiflorus	0.4/0.0		0.4/0.0									
Chrysothamnus nauseosus			4.7/10.0									
Tetradymia canescens			2.6/7.5					0.4/0.0				
PERENNIAL FORBS												
Dodecatheon conjugens	0.5/0.0											
Delphinium nuttalium	2.6/5.0	0.4/7.5										
Lomatium triternatum	0.1/2.5	0.1/2.5										
Frasera albicaulis	0.4/0.0	2.5/2.5										
Senecio interrigemus	3.1/10.0	0.1/0.0	6.0/0.0	0.1/0.0								
Achillea millefolium	0.6/7.5	0.3/5.0	3.5/10.0	0.5/2.5	0.7/10.0							
Lomatium grayi	1.7/10.0	2.1/17.5	2.7/0.0	11.8/35.0	13.4/32.5		15.1/22.5	0.4/2.5				
Erigeron sp.		0.4/0.0										
Chondrilla juncifolia			0.1/2.5									
Allium geyeri				5.9/37.5	0.2/0.0	18.6/45.0	22.6/55.0	0.8/2.5				
Grindelia nana				1.1/17.5		2.8/17.5	3.3/5.0	8.3/90.0		0.8/15.0	6.6/90.0	
PERENNIAL GRASSES/GRASSLIKES												
Elymus cinereus			37.4/52.5									
Festuca idahoensis	39.4/42.5	27.8/52.5			0.4/0.0							
Poa sandbergii	3.1/10.0	11.9/47.5	4.1/17.5									
Poa scabrella		0.1/2.5		38.1/92.5	30.1/85.0							
Agropyron spicatum			1.9/2.5									
Eleocharis palustris				3.1/20.0		10.5/42.5	4.3/10.0	14.1/50.0	15.8/35.0	31.7/0.0	5.3/17.5	63.6/95.0
Alopechurus geniculatus				0.1/2.5		0.1/0.0		0.4/2.5	0.7/15.0			5.1/80.0
Sitanion hystrix					2.8/10.0							

TABLE 1. Continued.

	% total cover / % frequency in 25% cover class											
Species	Zone 1 South	Zone 1 North	Zone 2 South only	Zone 3 South	Zone 3 North	Zone 4 South	Zone 4 North	Zone 5 South	Zone 5 North	Zone 6 South	Zone 6 North	Zone 7 North only
ANNUAL/BIENNIAL FORBS												
Plantago patagonica	4.9/50.0	0.9/5.0										
Plectricus macrocera	10.3/47.5	12.2/47.5	5.8/47.5		1.5/32.5							
Agoseris heterophylla	1.1/17.5	0.4/5.0	0.1/0.0	1.3/30.0	2.6/42.5	6.1/65.0	24.6/87.5	4.3/42.5	6.9/0.0			0.1/5.0
Draba verna	4.6/10.0	4.1/48.0	4.9/37.5	4.3/40.0	4.6/60.0	8.3/42.5		0.1/5.0	0.3/0.0			
Epilobium minutum	0.9/15.0	1.1/10.0	1.3/0.0	3.3/55.0	8.5/70.0	15.5/65.0	37.4/97.5	1.4/15.0	31.2/87.5			6.9/95.0
Montia linearis	2.2/12.5		0.2/0.0	3.9/60.0	1.5/25.0	0.8/0.0	0.1/0.0					
Holosteum umbellatum		1.0/2.5	1.3/7.5			0.1/2.5	3.3/5.0					
Veronica peregrina		0.1/2.5		0.8/12.5	2.0/17.5							
Lepidium perfoliatum			2.6/5.0			0.4/2.5						
Myosurus aristatus				0.1/2.5	0.1/2.5	2.3/0.0		5.3/60.0		2.1/17.5	0.9/7.5	15.5/75.0
Navarettia intertexta				0.2/0.0		1.0/2.5		18.3/100		23.5/97.5	20.3/100	1.6/12.5
Plagiobothrys scouleri				0.4/5.0	0.2/7.5	1.2/2.5		1.7/17.5		31.7/95.0	24.1/100	0.4/5.0
Lactuca serriola						0.6/15.0		0.1/0.0	0.3/2.5			0.4/7.5
Polygonum sp.						0.8/0.0	0.2/2.5	0.6/0.0		29.6/85.0	3.1/30.0	1.6/27.5
Psilocarphus oregonus						0.1/0.0		0.7/12.5		2.2/77.5	8.4/97.5	0.1/2.5
Downingia elegans								0.1/2.5	0.1/0.0	0.1/0.0	0.9/20.0	0.1/2.5
Boisduvalia stricta										2.3/32.5	1.6/42.5	
ANNUAL GRASSES/GRASSLIKES												
Bromus tectorum	1.1/15.0	1.2/18.0	4.3/22.5	0.6/5.0	1.1/7.5	2.8/12.5	0.2/0.0					
Deschampsia danthonioides	0.2/2.5	0.4/2.5		0.1/2.5		57.9/100	15.6/77.5	56.4/92.5	63.0/95.0	5.1/17.5	0.4/2.5	79.9/97.5
Festuca bromoides	1.9/27.5	0.7/17.5	0.3/7.5									
Agrostis diegoensis		0.1/5.0				17.6/75.0	3.3/55.0	9.1/65.0	0.1/2.5	0.1/2.5		0.1/0.0
Carex filifolia		0.1/0.0										
Bromus japonicus						0.4/25.0			0.2/2.5			

TABLE 2. Similarity index comparison of plant zones.

		Similarity index (frequency only)					
SOUTH POOL		Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6
Similarity index (weighted by cover)	Zone 1	***	57.9	42.1	25.0	26.3	7.0
	Zone 2	26.6	***	42.1	35.0	21.1	0.0
	Zone 3	11.9	12.2	***	65.0	68.4	41.4
	Zone 4	6.9	8.4	19.5	***	80.0	51.6
	Zone 5	2.7	2.3	9.8	66.4	***	62.1
	Zone 6	0.3	0.0	6.9	11.3	35.5	***

		Similarity index (frequency only)					
NORTH POOL		Zone 1	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7
Similarity index (weighted by cover)	Zone 1	***	50.0	34.3	28.6	11.1	21.6
	Zone 3	15.6	***	51.9	47.1	21.4	27.6
	Zone 4	4.4	36.4	***	62.1	43.5	50.0
	Zone 5	2.6	11.5	46.2	***	66.7	83.9
	Zone 6	0.6	0.4	9.1	23.2	***	72.0
	Zone 7	1.4	5.9	17.9	60.7	31.1	***

zone 2, for example, the average matric potential was –56 MPa in the 2–10-cm increment, –27 MPa in the 10–30-cm increment, and –2 MPa in the 30–60-cm increment.

On 23 April, when soils were moist, ECs were consistently higher in all plant zones and in both depth increments than they were on 28 June when soils had dried considerably (Fig. 6). Zone 2, the pool rim, had the highest ECs of any plant zone in the 10–30-cm increment on both the 23 April and 28 June sampling dates (Fig. 6). All mean ECs of saturation extracts, however, were below 2 dS/m, the minimum value for designation of a saline soil (Bohn et al. 1985). In the 2–18-cm soil increment of profile pit VP1 and the 30–48-cm increment of profile pit WR1, EC values were 2.20 and 2.62, respectively, indicating the potential for at least modest salinity in soils of the vernal pools.

The range of mean pH values of the 2–10-cm samples for each zone increased from 23 April (6.2 to 7.5) to 28 June (7.7 to 8.1; Fig. 6). pH values of the 10–30-cm, 30–60-cm, and 60–90-cm depth increments in zone 2 averaged 8.4, 9.1, and 9.3 over both dates, respectively. pH values of the WR1 soil profile pit, which has natric features, ranged from 7.3 to 7.9 among its horizons.

Sodium adsorption ratios (SAR) in soils of zone 2 of South Pool met the definition of sodic soil. Average SARs were 15.5 and 14.0 in the 10–30-cm depth increment on 23 April and 28 June, respectively (Fig. 6); 11.8 and 27.2 in the 30–60-cm increments on the earlier and later dates; and 27.4 in the 60–90-cm increment on 28 June. High SAR values in zone 2 of South Pool were in concert with moderately high SAR values of 9.7 in the 26–30-cm increment and 9.5 in the 30–48-cm increment of WR1. The SAR in the 2–10-cm increment of zone 3 was slightly higher than in other zones on 28 June.

DISCUSSION

Our study examined vegetation patterns and soil characteristics of vernal pools on the Marcellus site. Zedler (1987) suggested that the cycle of regional weather patterns is reflected in patterns of species germination and distribution in vernal pools. Monthly averages of precipitation, temperature, and evapotranspiration during our study season were fairly typical of the approximately 100-year climatic record in the Ritzville area; therefore, although we do not have data for many seasons, our data represent the vegetation structure and composition as expressed during a typical annual climatic pattern.

Cover-weighted similarity indices with two exceptions support the vegetation zone divisions we made at the outset of the study. It is not surprising that similarity indices based on frequency alone are inconclusive in that there were many species present in several zones. Cover values are a much better indicator of the strength of that presence. For example, although *D. danthonioides* had a high cover value in three different zones, each zone had a unique combination of co-occurring species:

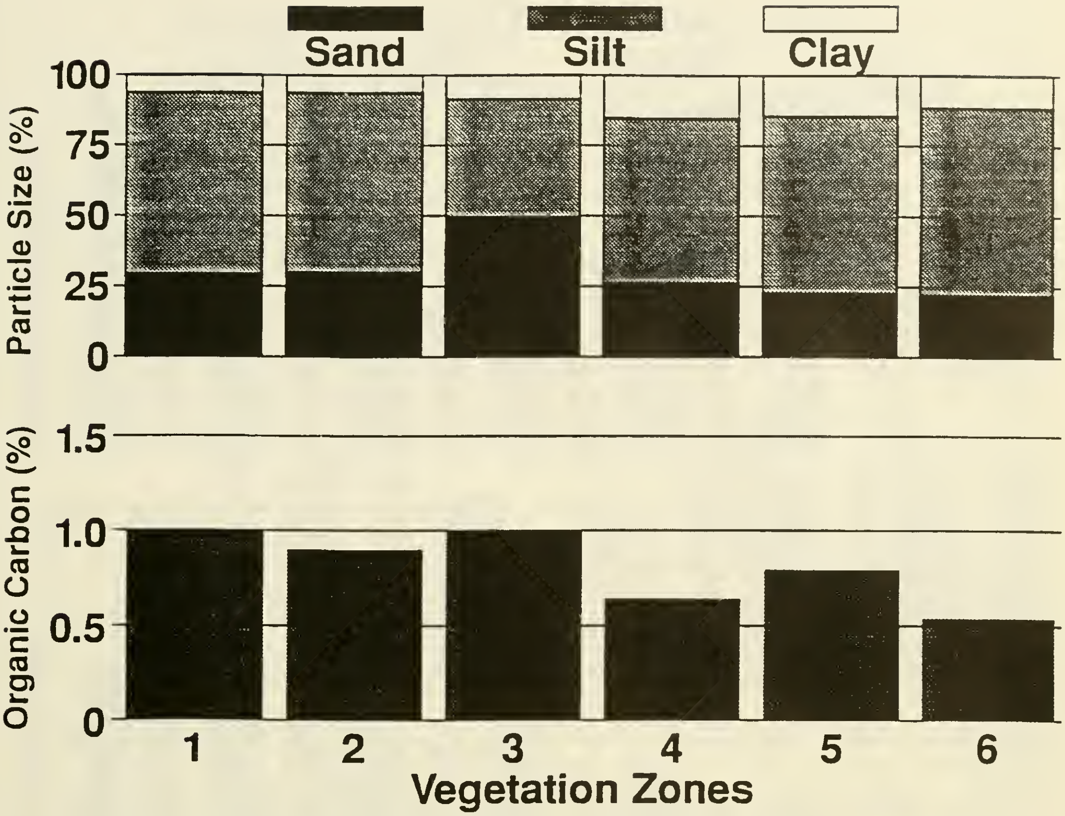

Fig. 4. Particle size and organic carbon content of the 2–10-cm depth of soils by vegetation zone in South Pool.

In zone 4, *A. geyeri*, *A diegoensis*, and *E. minutum* had highest cover values after *D. danthonioides*. In zone 5 those niches were filled by *N. intertexta* and *E. palustris*, and in zone 7 by *E. palustris* and *M. aristatus*.

Higher similarity indices between zone 4 and zone 5 (Table 2) reflect their position in the transition between drier upland-type communities and the pool basin area that contains standing water and/or has saturated soils more consistently and for a longer time period. We feel that species unique to each of these zones are ubiquitous and abundant enough to classify them as separate communities.

We found a greater ratio of annual to perennial species in wetter zones (zones 4–7) of the pools than in drier ones (zones 1–3). This tendency was also found in vernal pools in California (Holland and Jain 1977) and in a study of a seasonally flooded river marsh in Zimbabwe in which vegetation zonation was also reported (Cole 1973). It is difficult for perennials to withstand large changes in microenvironmental factors throughout the year, whereas the short life cycles of annual species may be completed within only one set of edaphic conditions. Annuals also produce abundant seeds, thus ensuring some survival due to variation in adaptability and the opportunity to delay germination until conditions are favorable.

Morphology and chemistry of the soils allow us to reconstruct the genesis of the pool system soils. Natric horizons have been documented as occurring in several situations in loessial soils across parts of the Columbia Plateau region where the mean annual precipitation is low to moderate (Peterson 1961). One specific situation is on the flanks of low mounds in areas of mound-and-swale microrelief where shallow soils are underlain by an impervious hardpan or bedrock. Calcium ion is presumed to become tied up as precipitated $CaCO_3$ in the calcic horizons of these soils over time. Apparently, water has moved laterally down the slope gradient within the mound soil during its genesis, transporting sodium ions and gradually concentrating them

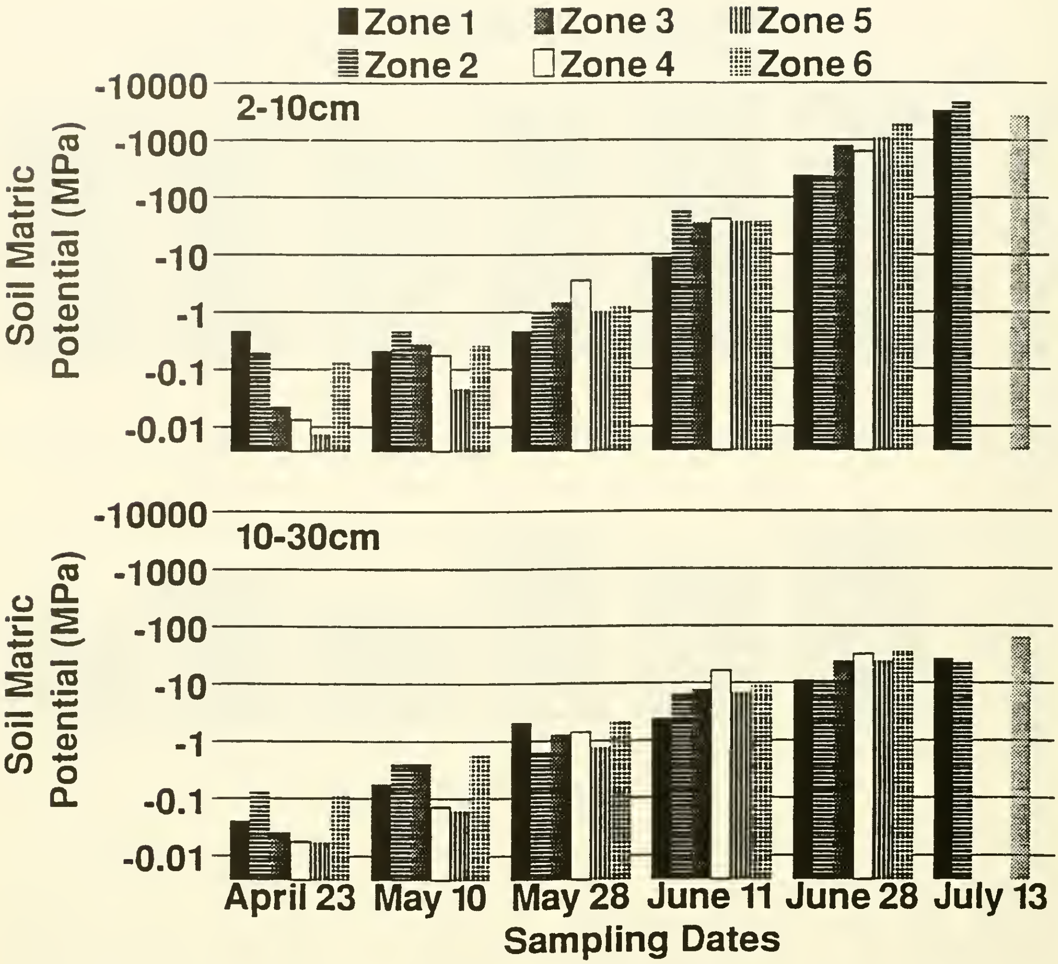

Fig. 5. Soil matric potential at 2–10-cm and 10–30-cm depth intervals by vegetation zone and sampling date in South Pool.

on the exchange complex of soil clays where the slope levels. Exchangeable sodium must accumulate to a critical level to effect the dispersion of clay colloids and organic matter, which in turn leads to the development of the typical natric soil morphology with a pale eluvial horizon overlying the clay-enriched, columnar-structured natric horizon. We observed a large variation in degree of expression of this morphology in pool-rim soils across the Marcellus site.

A natric horizon can have several adverse effects on the growth of plants. (1) When saturated, sodic soil horizons become dispersed and disaggregated, thereby clogging pores and preventing the flow of oxygen to plant roots. (2) When they dry, natric soils can form dense surface crusts that can prevent seedling emergence. (3) The availability of calcium, magnesium, and potassium can decrease in the soil due to preferential replacement of these ions by sodium on the exchange sites of clays and organic matter. (4) Sodium salts can create osmotic stress or be toxic to plants by interfering with their physiological processes (Black 1968).

Soil in zone 2 on the rim of the pools was not saturated during the part of the year when plants are physiologically most active, and the concentration of exchangeable calcium and magnesium was actually higher in zone 2 than in zone 1 (perhaps due to a higher cation exchange capacity in zone 2 soil). Osmotic stress and sodium salt toxicity appear to be the most likely conditions excluding zone 1 plants from zone 2, especially *A. tridentata*, whose roots

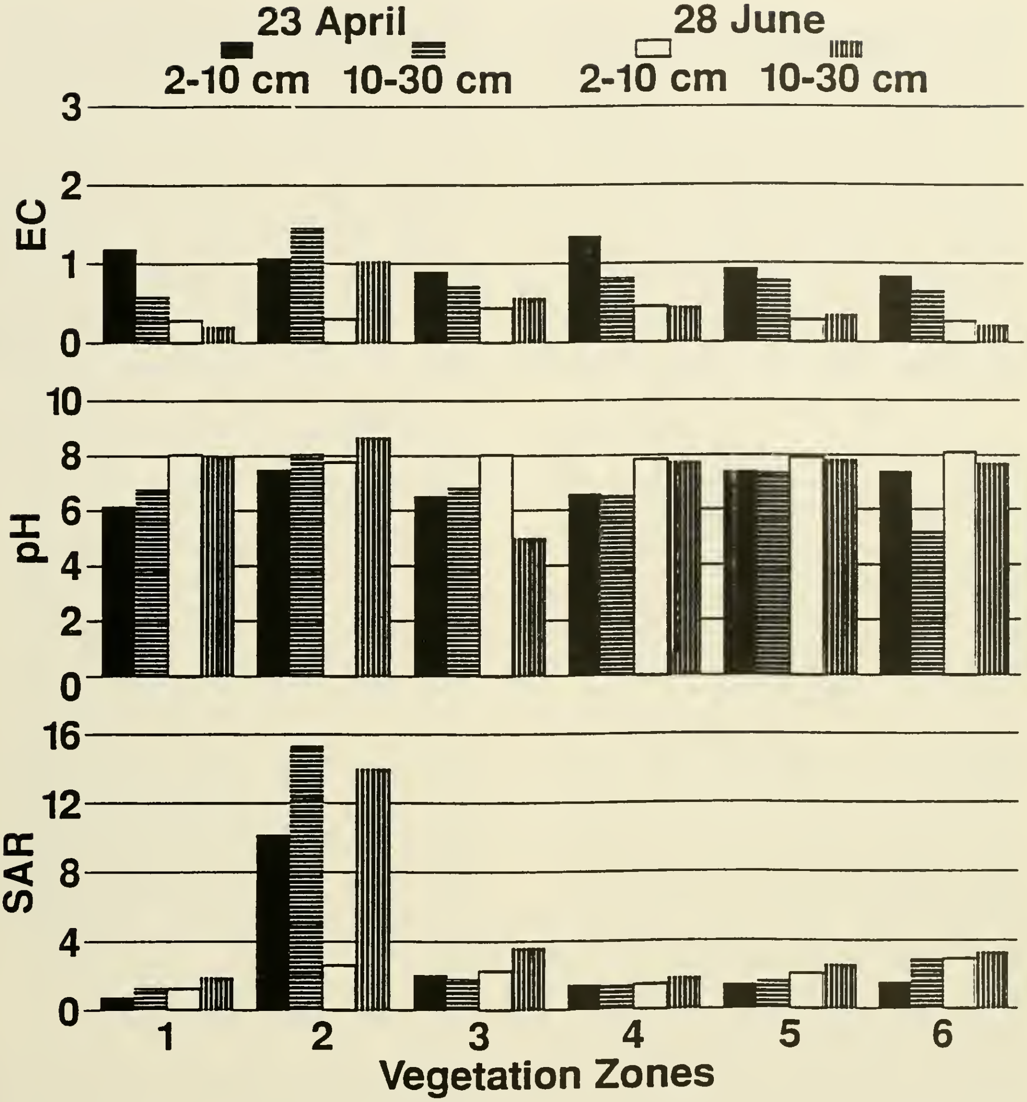

Fig. 6. Electrical conductivity (EC), pH, and sodium adsorption ratio (SAR) at 2–10-cm and 10–30-cm depth intervals by vegetation zone and sampling date in South Pool.

would penetrate to the most saline and sodic soil horizons. These conditions favor zone 2 plants such as *E. cinereus*. Choudhuri (1968) tested effects of soil salinity on *E. cinereus* and *A. tridentata* and found that *E. cinereus* was very tolerant of sodium salts and that *A. tridentata* was not. Surface crusts, high bulk density, and potassium deficiencies may also adversely affect zone 1 plants.

Although none of the ECs in South Pool were greater than 2 dS/m, soil salinity may have subtler influences on plant distribution. The 2 dS/m salinity limit is based on studies of crop plants, which generally are not native to the area in which they are grown. Limits of tolerance of native plants, such as *E. cinereus* as mentioned above, can be higher than in crop plants. Unfortunately, no specific studies exist of salinity tolerance of the species or genera found in vernal pool basins, either in California or Washington. Choudhuri (1968) found that all species he tested had a certain degree of self-adaptive capacity to increase their tolerance to salinity if the increase was gradual. Because plant tolerances to salinity can vary with environment (Levitt 1980), the interaction of slightly different salinity levels with changing moisture conditions may produce varying responses among the pool species. Some species will take up soluble ions through the cell walls of their roots, but the ions either will not pass through the cell membranes or will be stored inside cell vacuoles and thus not interfere with physiological processes in the plant (Levitt 1980). The decrease in soil ECs from the 23 April sampling date to the 28 June sampling date may be the result of plants preferentially taking up soluble ions to decrease their water potentials as soil water potential decreased.

Increased pH values from the first to the last sampling dates may indicate precipitation of alkaline salts. Again, specific responses of plants to this phenomenon can vary, and controlled studies of individual species would be necessary to make any further conclusions.

Our particle-size results coincide with those of California researchers (Lathrop 1976, Bauder 1987), who also found that finer particle sizes increased and sand fractions decreased from outside to the interior of the pool basins. Slightly more clay occurred in zone 4 soils than in zones 5 and 6 (the center of South Pool; Fig. 4), which is similar to the pattern in vernal pools on Kearny Mesa in California (Zedler 1987). A higher percentage of silt-sized particles can give a soil greater water-holding capacity under unsaturated conditions. The lack of a statistically significant difference in soil moisture potentials from the first to the last sample dates is difficult to understand. Given the generally large spatial variability in properties such as soil moisture potential, analysis of a greater number of samples would perhaps result in the finding of significant differences between dates and might also show significant differences among zones on particular sampling dates. It is interesting to note that some species were still surviving and in some cases photosynthesizing in soil matric potentials far less than –15MPa, commonly considered the permanent wilting point for plants. This seems to indicate an adaptability of vernal pool species to seemingly unfavorable moisture conditions.

Zedler (1987) stated that duration of standing water is the crucial factor in structuring plant distribution of vernal pools. The highly significant statistical difference we found between topographic elevation of the vegetation zones should be most closely related to the location and extent of above- and below-ground free water. We believe that soil moisture potential under unsaturated conditions probably also has a large effect on plant growth in the various vegetation zones. For example, different vernal pool species may have different types of root systems to take advantage of moisture in different parts of the soil profile, as was found in a study of several eastern Washington grasses (Harris and Wilson 1970). Also, maximum physiological activity can occur at different water potentials for different species (Wieland and Bazazz 1975). The duration of free-standing water and changes in unsaturated soil water potential through the season are probably both important to plant distribution in the pools.

Vernal pools can help us understand the physiological ecology of self-contained, water-controlled terrestrial ecosystems. We need to learn more about specific ecological processes in the vernal pool system to understand larger functions described so far. Future studies might include (1) examination of rooting systems and their relationship to water use and availability, (2) determination of the minimum physiologically detrimental salinity (especially of various sodium salts) and optimal pH levels for individual species, and (3) tolerance of individual species to varying durations of standing water and levels of unsaturated soil moisture potentials.

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GOLDEN EAGLE (*AQUILA CHRYSAETOS*) POPULATION ECOLOGY IN EASTERN UTAH

J. William Bates[1] and Miles O. Moretti[1]

ABSTRACT.—Golden Eagle population ecology was studied from 1982 to 1992 in eastern Utah where over 47% of 233 territories monitored during the study period were active. Golden Eagle use of four habitat types was compared. Talus territories were used less often than expected; valley, aspen-conifer, and pinyon-juniper territories were used as expected. Number of young produced per territory averaged 0.612 and was correlated with rabbit abundance. Observations on the impacts of coal mining at two locations are discussed.

Key words: Aquila chrysaetos, *Golden Eagle, population, habitat use, prey relationships.*

The Golden Eagle (*Aquila chrysaetos*) is a year-round resident of eastern Utah but is most common during the nesting season. Golden Eagle nests in the area are found at elevations of 1546 m (5070 ft) to 3000 m (9800 ft). Most are located on cliffs, while others are located in cottonwood (*Populus fremontii*) and Douglas fir (*Pseudotsuga menziesii*) trees. Golden Eagle eyries are found in riparian areas, shadscale-clay hills, pinyon-juniper hills with sandstone cliffs, steep talus slopes with large cliffs, and aspen-conifer areas in trees or on smaller cliffs (Jensen and Borchert 1981).

Many nests are located on prominent escarpments found in the Castle Valley area. These escarpments are part of the Castle Gate and Hiawatha formations, which are rich in coal deposits (McGregor 1985). Coal mining is a major industry in the area, and mining activities have the potential to impact nesting Golden Eagles. As a result, federal land-management agencies have required mining companies to monitor eagle nests on their properties.

The primary objective of this project was to monitor Golden Eagle and eagle prey populations in a variety of habitats in eastern Utah. The secondary objective was to summarize data collected by mining companies required to monitor raptor nests.

STUDY AREA

Golden Eagle nests monitored during this study were located in Carbon and Emery counties in eastern Utah (Fig. 1). The study area includes territories from Scofield and Emma Park south to Quitchipah Creek, and from Horse Canyon on the east to Huntington Canyon on the west. Elevations in the study area range from 1546 m (5070 ft) to 3000 m (9800 ft). Vegetative zones include riparian, saltbush (*Atriplex* sp.), sagebrush (*Artemisia* sp.), pinyon-juniper (*Pinus edulis, Juniperus osteosperma*), and mixed aspen-conifer.

The study area was classified into four habitat types that typify eagle use in the area: (1) **valley territories**, located on saltbush flats, on clay hills, or along riparian areas, with nests in cottonwood trees, on conglomerate pinnacles, or on clay ledges; (2) **pinyon-juniper territories**, with nests found on sandstone cliffs; (3) **talus territories**, where eyries were located on thick sandstone cliffs; and (4) **aspen-conifer territories**, where one nest was located in a Douglas fir and all others were on sandstone cliffs.

METHODS

The U.S. Fish and Wildlife Service, in cooperation with the Utah Division of Wildlife Resources (UDWR), conducted extensive helicopter surveys in 1981 and 1982 to locate Golden Eagle nests in the area. Over 250 nests were located and monitored during these surveys. Beginning in 1986 several mining companies were required to monitor approximately 26 territories within a 10-mile radius of the areas affected by mining to assess the impacts of coal mining on the local Golden Eagle population. In 1990 the UDWR began monitoring

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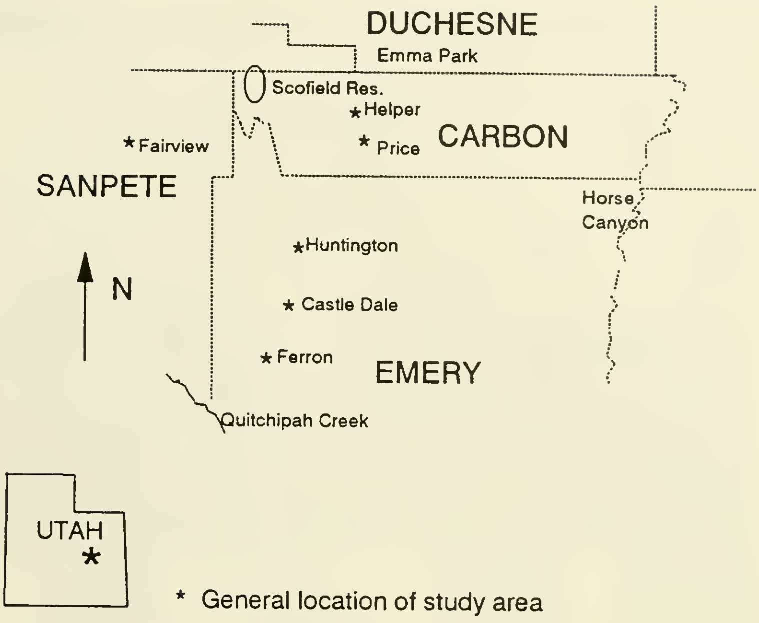

Fig. 1. Map showing Golden Eagle study area.

an additional 13 territories beyond the 10-mile radius impact area. A total of 39 territories were monitored in 1992.

A Bell Jet Ranger helicopter with a pilot and two observers was used to check all known nests in the area affected by mining. Previously unknown nests occasionally were found and recorded during these flights. Normally, the helicopter was able to fly close enough to allow direct observation of the nest. Adult eagles usually would remain in the nest as the helicopter passed, although occasionally they flushed. Adult eagles also left the nest area when they were viewed from the ground.

Eyries in nonimpacted areas were observed from a distance to determine whether eagles were present. If adult eagles, greenery, or fresh mutes were present, the nest site was classified as **occupied**. If young or eggs were present, it was classified as **active**. The nest was classified as **inactive** if no sign of eagle use was present. If eggs were present but failed to hatch, or if all nestlings were observed to die before fledging, it was classified as **failed**. Due to commitments to other projects, we had insufficient time to return to each territory to determine the number of successfully fledged young. Therefore, these data cannot be interpreted to indicate Golden Eagle recruitment or nesting success.

Rabbit populations were monitored in the area to determine prey base trends during 1986–91. Eleven 5-mile transects were completed each year in the study area. Transects were conducted just after dusk or just before dawn by mounting a spotlight on a vehicle and recording all rabbits seen on one side of the road. Transects were completed in desert shrub, pinyon-juniper, sagebrush, and aspen-conifer habitat types.

Data were analyzed using descriptive statistics, contingency table analysis, and linear regression in the Number Cruncher Statistical System (Hintze 1990). The Bonferroni Z test (Neu et al. 1974) was used to analyze utilization data.

RESULTS

Habitat Use

Of 233 Golden Eagle territories checked from 1981 to 1992 (average/year = 26), 109 (47%) were active and produced young. Almost 78% of the territories were occupied. The year with the most active territories (56%) was 1990 (Fig. 2). In that same year 94% of monitored territories were occupied. The year with the fewest known active territories (33%) was 1988.

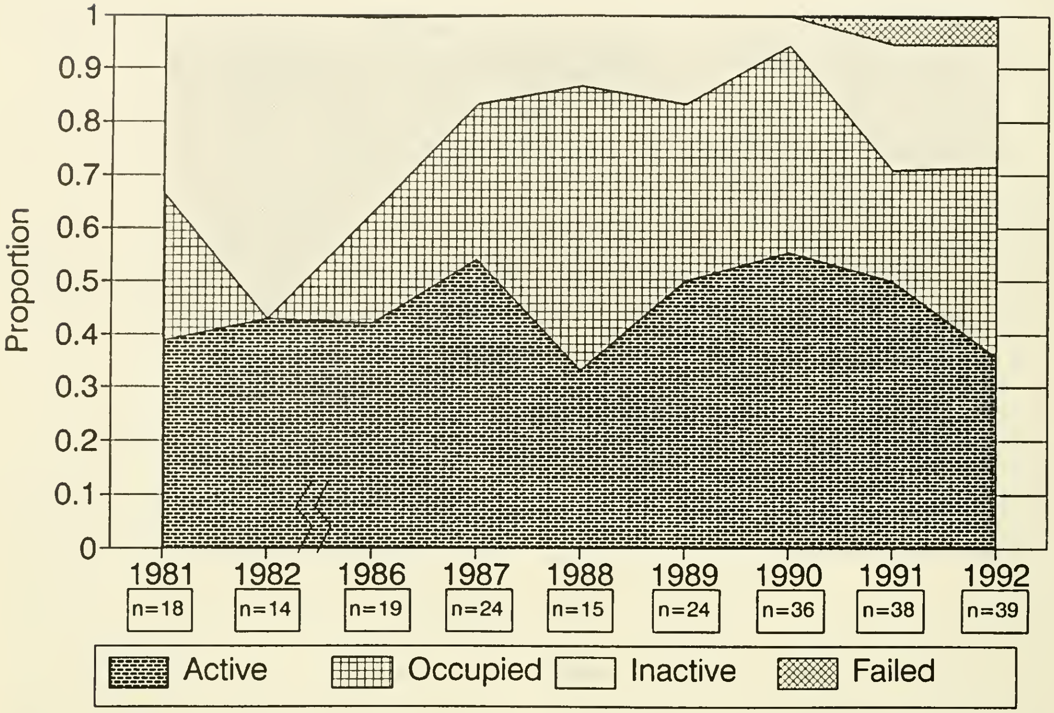

Fig. 2. Status of Golden Eagle territories in eastern Utah.

Of 185 territories checked in consecutive years, over 28% (52) were active. Five territories were observed to produce young for 3 consecutive years. One territory was active 4 consecutive years, while another produced young 5 consecutive years. One territory failed 3 years in a row. Generally, eagles use different nest sites within the same territory in consecutive years, but in our study eagles used the same nest as the previous year 11 times (21%).

Golden Eagle nesting activity was analyzed by habitat type. A significant difference was found between the four habitat types (chi-square = 20.6, $P < .015$). The number of active territories in each habitat type was compared to the expected number active using the Bonferroni Z statistic (Neu et at. 1974). Talus territories were active less frequently than expected, accounting for almost 37% of available habitat, but only 24% of active territories (Table 1, Fig. 3). The number of active nests in valley, pinyon-juniper, and aspen-conifer territories did not differ significantly from the number expected.

Talus eyries had their highest incidence of use in 1982, 1987, 1990, and 1991, with over 40% of territories active. In 1989 only one of nine talus territories was active. Over 75% were active in 1986, 1987, 1989, 1991, and 1992. Six of nine were active in 1990, seven of nine in 1991 (although two eyries failed), and seven of nine in 1992. Two or fewer valley territories were checked in 1981, 1982, and 1988. Over 57% of aspen-conifer territories were active each year, with the exception of 1982, 1986, and 1992, when only one of three, one of four, and three of nine, respectively, were active.

Nesting was relatively late in 1991 because of an unusually wet and cold spring; precipitation was 4.34 cm (1.71 in) greater than normal and temperatures were 1.65°C (3°F) cooler than the 30-year average at the Hiawatha weather station. Golden Eagles also showed a shift in habitat use in 1991. All known valley tree nests were active (n = 9). Talus territories were used less than expected and were initiated up to 4 weeks later in 1991 than in 1990. In spite of the cool spring, all four known aspen-conifer territories over 2400 m in elevation near Joe's Valley Reservoir were active and began incubation earlier than lower talus territories and close to the time incubation began at this elevation in previous years.

TABLE 1. Active Golden Eagle eyries by habitat type in eastern Utah, 1982–92.

Habitat type	Sample points	Proportion of habitat	Territories active	Expected active	Prop. of active territories	95% confidence interval
Valley	51	0.219	32	24	0.294	$.196 < p < .392$
Pinyon/juniper	41	0.176	22	19	0.202	$.116 < p < .288$
Talus	85	0.364	26	40	0.239	$.147 < p < .331$*
Aspen/conifer	56	0.241	29	26	0.266	$.171 < p < .361$
Total	233	1	109	109	1.001	

*Fewer territories active than expected.

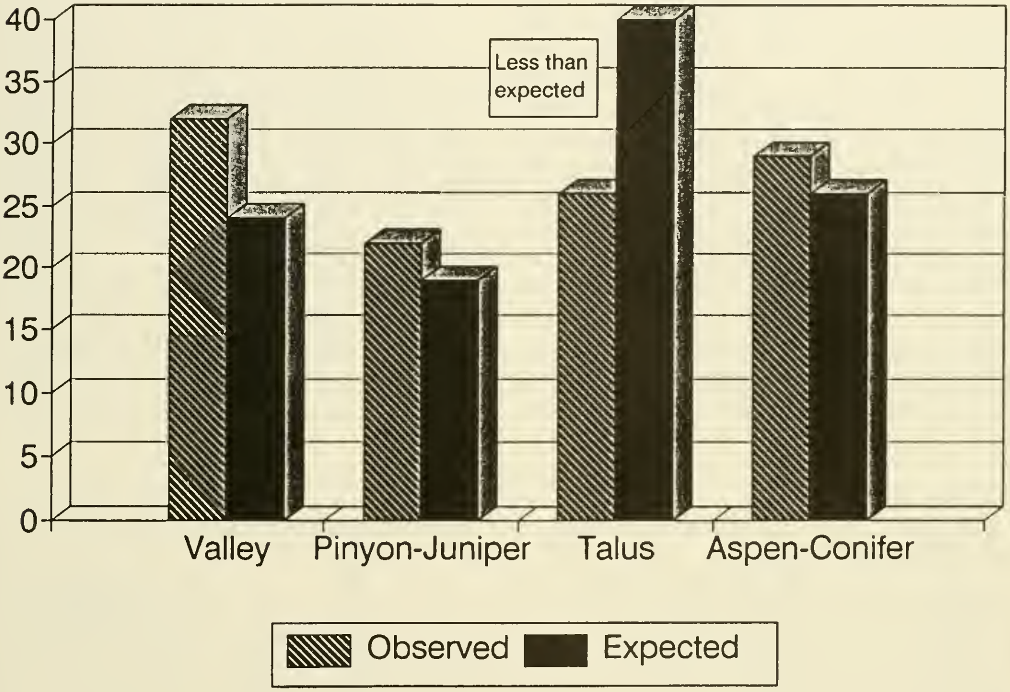

Fig. 3. Active Golden Eagle eyries by habitat type in eastern Utah.

Only 2 of the maximum 39 territories monitored in any one year were documented as being impacted by mining activities. Energy West Mining applied for and received a permit from the U.S. Fish and Wildlife Service to 'take' eagle nests in Newberry Canyon. This was necessary because of coal removal directly under a major escarpment that had four eagle nests on it; a major spauling was a possibility. Plateau Mining faced a similar situation at Star Point and also obtained a U.S. Fish and Wildlife Service permit to take two nests because of escarpment failure.

To keep Golden Eagles from using the two nests at Star Point, both nests were covered with chain-link fencing in 1989. From 1985 to 1988 this territory was active twice, occupied once, and inactive one year. In 1989 the eagle pair built a new nest in a pine tree about 300 m from the cliff nests but produced no young. In 1990 and 1992 the pair used an alternative cliff nest about 500 m from the fenced cliff nests and produced one young each year. In 1992 this nest was tended, but nesting did not occur. This territory produced young 2 of 4 years before and 2 of 4 years after the nests were fenced.

Escarpment failure in Newberry Canyon resulted in the loss of three nests in 1989. One nest remained in 1989 and was used to produce two young. This nest fell before the spring of 1990. This territory produced young

2 of 4 years before the nests were lost and 1 of 4 years after the escarpment failure. Five other Golden Eagle territories are located within 8 km airline distance of Newberry Canyon. These territories produced young 39% of the time before the spauling, compared to 55% after. Although Newberry Canyon territory was not active again until 1993, these territories averaged 2.25 pairs active/year producing young before the nests fell, and 3 active/year after the spauling.

Productivity

Rabbit transects were conducted in the area from 1986 to 1991 (Bates 1989). Data on rabbit populations prior to 1986 are available through harvest statistics compiled by the UDWR (Mitchell and Roberson 1992). Number of cottontail rabbits harvested per hunter day was highest in 1982 and declined dramatically in 1984 (Table 2). Rabbit populations remained low until 1987, when they began to increase.

Average number of eaglets produced per territory was 0.612 (SE = 0.059) over the period 1981–92. Number of young produced per territory was above average in 1982, 1989, 1990, and 1991 (Fig. 4), although there was not a significant difference in number of young produced among years ($P = .27$). Except for 1991, these years coincided with increased rabbit populations (Table 2). Years with the highest number of young produced per active territory were 1982 and 1989, which were years with peak rabbit numbers. Although, based on transects, rabbit populations declined in 1990 and 1991, the number of young per territory was above average (Fig. 4) because the percentage of active territories was above average (Fig. 2).

TABLE 2. Rabbit indices in eastern Utah, 1982–91.

Year	Cottontails per hunter day	Cottontails and jackrabbits/mile
1982	1.81	
1983	1.79	
1984	0.9	
1985	0.77	
1986	0.93	0.17
1987	1.37	0.39
1988	1.55	0.75
1989	0.93	0.86
1990	1.28	0.56
1991	1.5	0.43

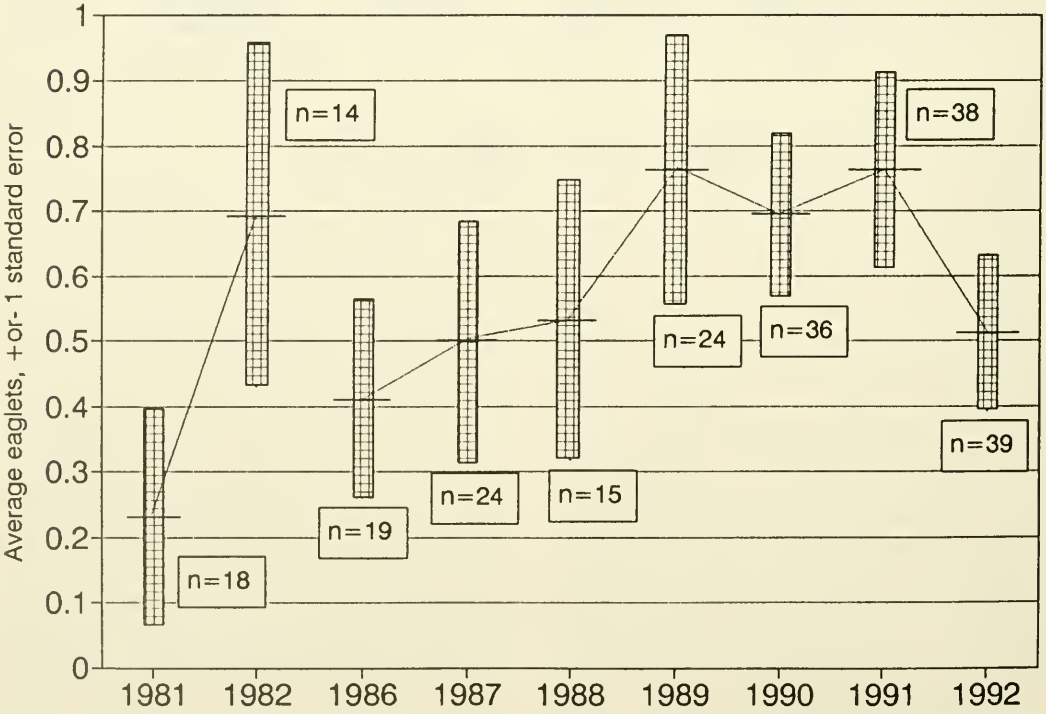

Fig. 4. Average number of young per territory in eastern Utah.

Linear regression was used to determine if there was a relationship between number of rabbits seen per mile during rabbit transects in 1986–91 and number of eaglets per territory. A weak relationship was found (R^2 = .33, P = .24), indicating that part of the variability in Golden Eagle productivity was explained by rabbit population levels. The data indicated a lag effect, with productivity higher the year after rabbit populations increased (Fig. 5). By using linear regression to test this hypothesis, we found a near-significant relationship between number of rabbits the previous year and number of eaglets per territory (R^2 = .63, P = .058; Fig. 6). A significant relationship was also found between number of rabbits/mile and number of young produced per active territory in the same year, indicating higher production in years when rabbits were more abundant (R^2 = .83, P = .01; Fig. 7). These data demonstrate that Golden Eagles produce more young in the same year that rabbit populations increase, but a higher proportion of territories are active the year following an increase in rabbits (Fig. 5).

DISCUSSION

Number of young produced per territory and proportion of active territories in southeastern Utah were similar to those of other studies. Phillips et al. (1990) found 0.78 young produced per occupied territory in Montana and Wyoming from 1975 to 1985, compared to 0.82 in this study. They also found 1.46 young produced per successful territory, compared to 1.39 per active eyrie in this study. Results from southeastern Utah are inflated as the Phillips study was based on number of fledged birds and this study recorded only the number present in nests. However, most eaglets in this study were approaching fledging age when observed. Murphy (1975) found 0.69 young fledged per occupied territory in central Utah.

Number of eaglets produced was associated with rabbit population densities in the study area. Although other prey, such as white-tailed prairie dogs, are available, correlations with rabbit populations were quite high.

High rabbit populations seemed to influence Golden Eagle nesting in two ways. First, number of young produced per active nest was

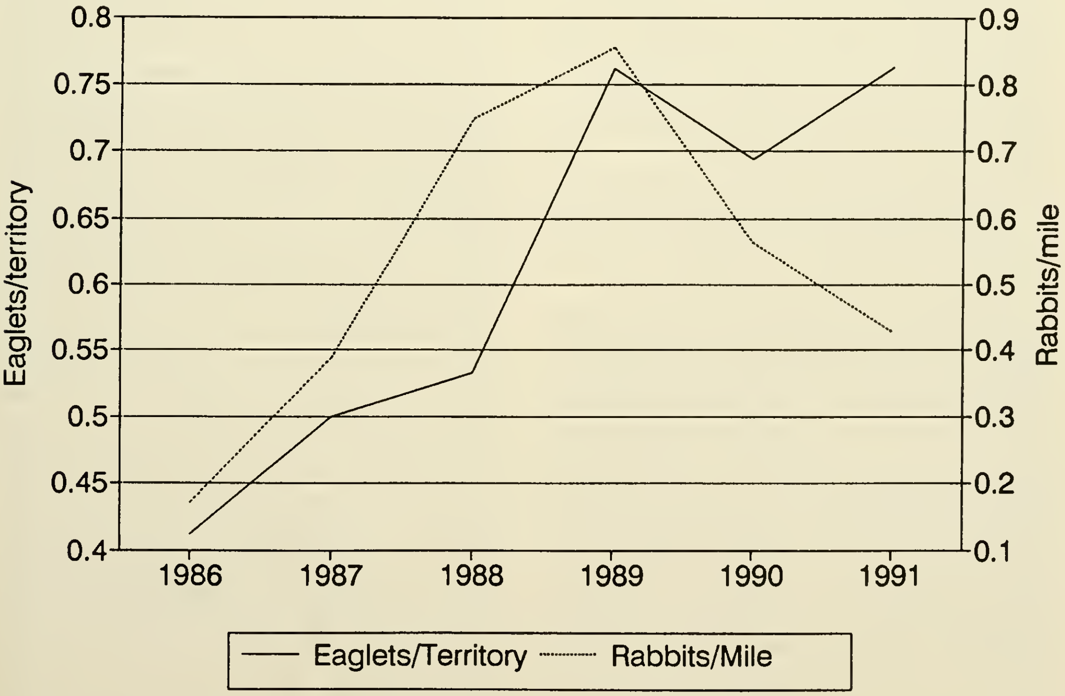

Fig. 5. Golden Eagle production and rabbit population trends.

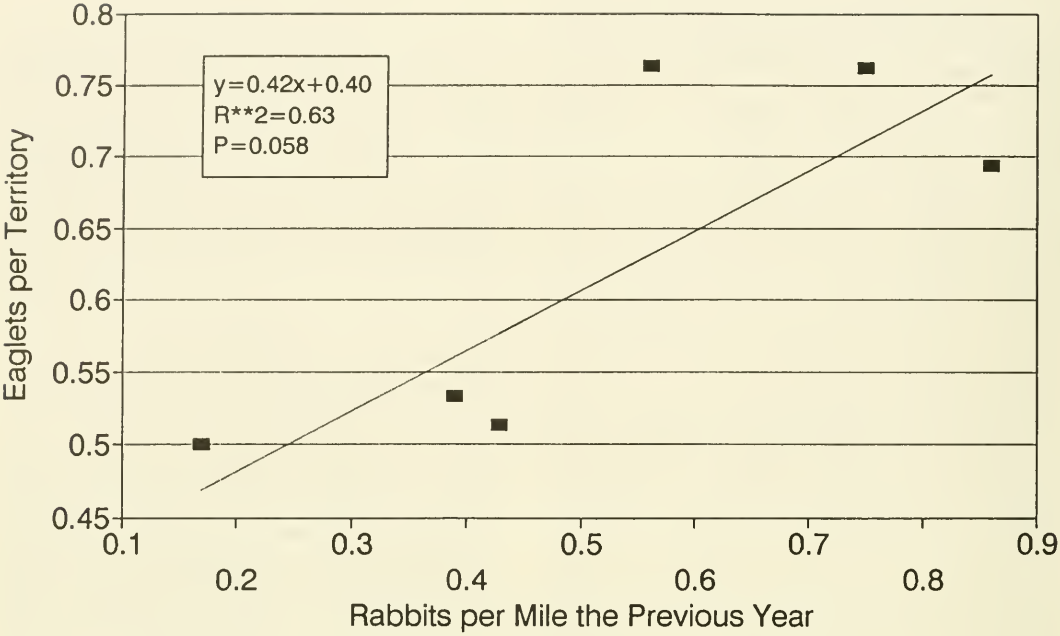

Fig. 6. Eaglets per territory as a function of rabbits the previous year.

affected by number of rabbits in the area that year; i.e., more eaglets were produced in years with higher rabbit populations. This relationship has also been found in other studies (Murphy 1975, Phillips et al. 1990). Second, there appeared to be a lag effect on number of eagles that attempted to nest. There was a significant correlation between number of young produced per territory and number of rabbits the previous year. High rabbit populations may have allowed more pairs in the area to nest, or enticed more eagles into the area, resulting in an increased number of active territories.

Use of valley territories increased in years with higher rabbit populations. Golden Eagles may have selected nest location to minimize the energy required to obtain food. In years with higher rabbit populations, eagles may have spent more time hunting in valley locations. The 2 years with the fewest active talus eyries, 1988 and 1989, were years of relatively high rabbit abundance. Eagles possibly avoided talus eyries in years of high rabbit populations because they were too far from an abundant food source. In years with fewer cottontail and jackrabbits they may have used these territories to take advantage of other prey, such as snowshoe hares or woodrats.

Data on mining impacts caused by cliff spaulings are too few to draw empirical conclusions. However, we offer some observations. When ample suitable habitat is nearby, there appeared to be no net loss in production. The territory at Star Point was active 2 of 4 years before and after the escarpment failure. Although the pair at Newberry Canyon did not re-nest in the canyon for 3 years after the original nests fell, they may have been using alternate nests of adjoining pairs. The five territories in the area averaged 2.25 pairs active/year before and 3 active/year after the escarpment failure.

In consideration of these observations, we offer several recommendations to protect against loss of birds or territories. First, if spauling can be controlled, it should be done in the nonnesting season. Otherwise, physically fencing may help prevent loss of nestlings. The two fenced nests were not used; however, the pair built a new nest below a fenced nest on a cliff that was failing. The pair did not attempt to raise young in that nest. Second, there must be ample suitable nesting habitat to allow other nests to be built. In Newberry Canyon a sheer wall was the result of escarpment failure and may not provide suitable nesting structure. This pair built a new nest 150 m east of a

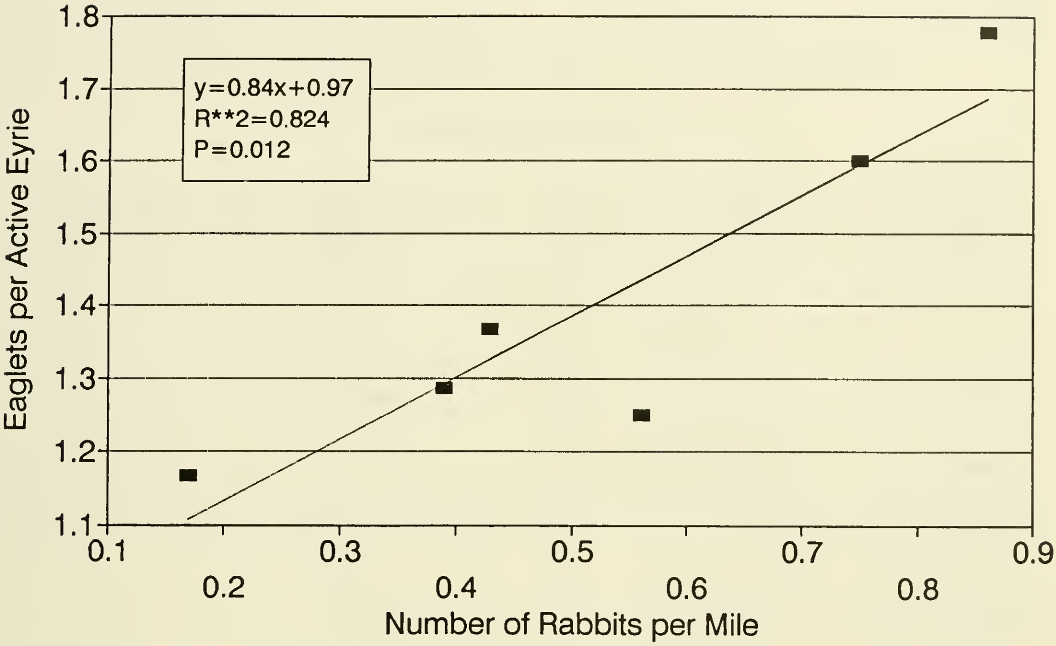

Fig. 7. Eaglets per active eyrie as a function of rabbits, eastern Utah.

fallen nest on a ledge that did not fail. Loss of nesting structure could be a consideration in areas with limited cliff habitat where the whole face fails.

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IDENTIFICATION OF *PURSHIA SUBINTEGRA* (ROSACEAE)

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ABSTRACT.—Populations of *Purshia* in central Arizona are intermediate in some characters between *Purshia subintegra*, an endangered species, and *Purshia stansburiana*, the common cliffrose. These intermediates may represent forms derived from a history of hybridization and introgression between the putative parent species. Morphological data were obtained from 216 pressed specimens of *P. subintegra*, *P. stansburiana*, and introgressed forms. Over 50 separate discriminant function analyses (DFA) and principal components analyses (PCA) were run on numerous combinations of raw and log-transformed data. The best variable suite, providing the clearest discrimination between groups, used log-transformed data on 15 morphological characters, but DFA post-hoc identifications were 90–100% correct with only 7 characters using raw data. DFA distinguished four separate nodes of variation. Two groups consisting of 122 *P. subintegra* and 29 *P. stansburiana* were easily discriminated in DFA and were distinguished in PCA as well. Introgressed forms were consistently identified in two much less well-defined groups of 46 and 19 specimens. Introgressed forms are not intermediate between the two supposed parents in some characters, appearing most similar to *P. stansburiana* in most measured characteristics. Principal distinguishing characteristics of the four groups are as follows: *P. subintegra*—usually eglandular, has 0–2 leaf lobes and short hypanthia-pedicels; *P. stansburiana*—always abundantly glandular, has 4 leaf lobes and short hypanthia-pedicels; the introgressed form "Tonto" is usually eglandular, has 4 leaf lobes and long hypanthia-pedicels; the introgressed form "Verde" is usually glandular, has 4 leaf lobes and slightly shorter hypanthia-pedicels.

Key words: Purshia subintegra, Purshia stansburiana, *Arizona cliffrose, cliffrose, endangered species, morphometrics, introgression, taxonomy,*

Purshia subintegra (Kearney) Henrickson (Arizona cliffrose) is protected under federal law as an endangered species (USFWS 1984). For a federally endangered species like *P. subintegra* it is important, indeed vital, to know the taxonomic identity of every individual plant in a given population because the protective measures of the Endangered Species Act are available to species (including forms that exhibit characteristics of introgression with other species), but not to their early generation hybrids.

Purshia subintegra is found in four widely scattered locations from northwestern to southeastern Arizona (Table 1, Fig. 1). The first collection was made by Darrow and Benson in 1938 (Kearney 1943, Schaack 1987a) near Burro Creek in Mohave County, Arizona. A second population was documented in a collection by Pinkava, Keil, and Lehto in 1968 (Pinkava et al. 1970) almost 300 km from Burro Creek, near Bylas in Graham County, Arizona. Anderson (1986) found a third population on bluffs overlooking the upper Verde River near the town of Cottonwood (referred to as the Verde Valley area) and reported on Barbara G. Phillips' 1984 discovery of the fourth locality for *P. subintegra* near Horseshoe Dam along the lower Verde River.

At the four locations cited above, *Purshia subintegra* is restricted to outcrops of Tertiary deposits of limy lacustrine rock formations (Anderson 1986). Soils derived from these ancient lake basin rocks are characterized by low nitrogen and phosphorus levels, which limit, or preclude, typically Sonoran Desert species that are common on nearby sites with soils derived from igneous and metamorphic rocks (Anderson 1986). *Purshia subintegra* is a species of the northern and eastern perimeter of the Sonoran Desert; all four sites supporting the species are at or below 1000 m elevation.

Purshia stansburiana, the common cliffrose of the Southwest, is not a Sonoran Desert species and consequently is not sympatric with *P. subintegra* at three of the four *P. subintegra* sites known. In the Verde River Valley of eastern Yavapai County, Arizona, the highest-elevation *P. subintegra* site, the two species occur in close enough proximity that gene exchange may occur, at least occasionally. Scattered populations and individuals of

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TABLE 1. Locations of *Purshia* spp. collections sampled in multivariate morphometric analysis; 216 specimens collected for morphological analysis in Arizona.

Region and collection site	*N*	County	Letter designation	Elev. (m)	Biotic community	Substrate
Purshia subintegra						
1. Bylas	20	Graham	A	850	Sonoran desertscrub	Tertiary lacustrine
2. Burro Creek	20	Mohave	B	790	Sonoran desertscrub	Tertiary lacustrine
3. Horseshoe Lake	42	Maricopa	C	640	Sonoran desertscrub	Tertiary lacustrine
4. Verde Valley	8	Yavapai	D	1025	Semidesert grassland	Verde Formation
5. Verde Valley	24	Yavapai	E	1050	Semidesert grassland	Verde Formation
6. Verde Valley	8	Yavapai	F	1065	Semidesert grassland	Verde Formation
"Verde"						
Verde Valley						
7. DK Well Rd.	3	Yavapai	a	1185	Semidesert grassland	Verde Formation
8. Seventeen Tank Rd.	6	Yavapai	b	1020	Semidesert grassland	Verde Formation
9. Mesa Blanca	3	Yavapai	c	1210	Semidesert grassland	Verde Formation
10. DK Well Rd.	1	Yavapai	d	1175	Semidesert grassland	Verde Formation
11. DK Well Rd.	3	Yavapai	e	1155	Semidesert grassland	Verde Formation
12. Seventeen Tank Rd.	3	Yavapai	f	1035	Semidesert grassland	Verde Formation
13. Cottonwood Hwy.	1	Yavapai	g	1030	Semidesert grassland	Verde Formation
14. Cornville	2	Yavapai	h	1110	Semidesert grassland	Verde Formation
15. Black Mtn. Rd.	6	Yavapai	i	1385	Piñon-juniper woodland	Supai Formation
16. Cherry Rd.	3	Yavapai	j	1070	Semidesert grassland	Verde Formation
17. Cherry Rd.	3	Yavapai	k	1230	Interior chaparral	Verde Formation
18. Cherry Rd.	6	Yavapai	l	1270	Interior chaparral	Verde Formation
19. Cherry Rd.	6	Yavapai	m	1341	Interior chaparral	Verde Formation
"Tonto"						
Verde Valley						
20. Camp Verde	2	Yavapai	n	990	Interior chaparral	Verde Formation
South of Globe						
21. Dripping Springs Rd.	6	Gila	o	990	Semidesert grassland	Limestone?
Tonto Basin						
22. Pinal Creek	3	Gila	p	944	Semidesert grassland	Tertiary lacustrine
23. Punkin Center	6	Gila	q	725	Sonoran desertscrub	Tertiary lacustrine
24. Beeline Hwy.	2	Gila	r	1015	Interior chaparral	Tertiary lacustrine
Purshia stansburiana						
25. Jerome	16	Yavapai	X	1770	Interior chaparral	Tertiary basalt
26. Skull Valley	3	Yavapai	Y	1270	Semidesert grassland	Weathered volcanics
27. Sonoita	10	Santa Cruz	Z	1435	Plains grassland	Quaternary alluvium

Purshia in central Arizona exhibit what appear to be intermediate characteristics between *P. subintegra* and *P. stansburiana*. Numerous botanists (Schaack and Morefield 1985, Schaack 1987a, 1987b, Anderson 1986, 1993, Henrickson personal communication 1988) have assumed that intermediate forms arose from past hybridization and subsequent introgression with one or both of *P. subintegra* and *P. stansburiana*, and that hybridization and introgression may still be occurring in some locations. Throughout this paper the term "introgressed form," recognizing that the origin of the intermediates is still unclear, is applied to forms that are intermediate in some characters between *P. subintegra* and *P. stansburiana*.

Related Taxa

The systematics of *Purshia* is under investigation by Dr. James Henrickson for the upcoming Chihuahuan Desert Flora and the revised Arizona Flora. Henrickson (1986) published a brief note recombining species previously placed in *Cowania* to *Purshia*, a move generally agreed upon by botanists. Thus, the genus *Purshia* now consists of seven species: *Purshia ericifolia* (Torr. ex Gray) Henrickson, *P. glandulosa* (Curran), *P. mexicana* (D. Don) Henrickson, *P. plicata* (D. Don in Sweet) Henrickson, *P. stansburiana* (Torr. in Stansb.) Henrickson, *P. subintegra* (Kearney) Henrickson, and *P. tridentata* (Pursh) DC. Although the

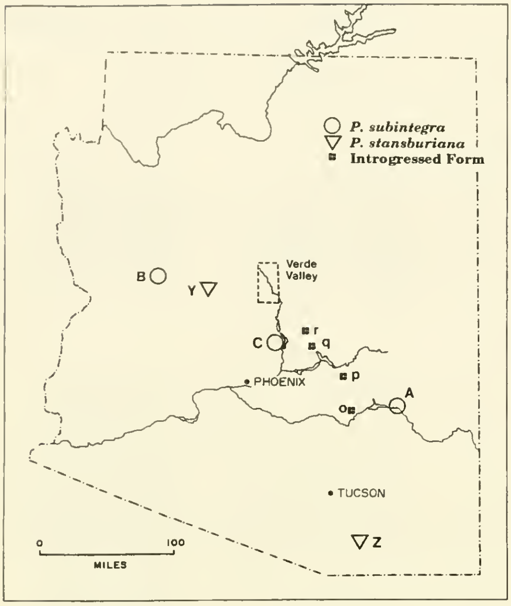


Fig. 1. Distribution of sampling sites, species, and introgressed forms. See Figure 2 for an expanded view of Verde Valley. Letters identify sites illustrated in graphs of multivariate analyses.

relationship of *P. subintegra* to *P. stansburiana* is the subject of this study, that of *P. subintegra* to the morphologically similar *P. ericifolia* is of interest as well. All other *Purshia* taxa have lobed leaves except *P. ericifolia*. Leaves of *P. ericifolia* are about 6 mm long, simple, acute, linear, and eglandular. The species is restricted to limestone outcrops in the Texas Big Bend region. It has been speculated that *P. subintegra* may have evolved from some ancient series of crosses and backcrosses involving *P. ericifolia* and some other *Purshia*, perhaps *P. stansburiana* (McArthur et al. 1983). Phylogenetic investigation of the whole genus in relation to closely related genera such as *Fallugia* would be valuable in interpreting *P. subintegra* and should be the logical next step for future work.

Relation to *Purshia stansburiana*

Schaack (1987a, 1987b) suggested that the basionym *P. subintegra* was based on material of hybrid origin, resulting from past hybridization of *P. stansburiana* and a previously unnamed central Arizona *Purshia*. He consequently published a new species name, *Purshia pinkavae* Schaack, to include a very pure concept of what had been included in *P. subintegra*, ". . . restricted to late Tertiary calcareous, lacustrine deposits ca. 16–21 km northwest of Bylas, Graham County, Arizona."

Few botanists have adopted Schaack's taxonomy, but most recognize that variation is present and concede that it may have resulted from some form or degree of past hybridization or introgression involving *P. subintegra* and *P. stansburiana*.

McArthur et al. (1983) reported n = 9 and 2n = 18 for *P. subintegra* and *P. stansburiana*, respectively. Phillips et al. (1988) used starch gel electrophoresis to investigate isozymes at 14 loci in three populations of *Purshia stansburiana* and four populations of *P. subintegra*. The material used in this study was collected by the author and preserved in liquid nitrogen from the same plants that provided dried specimens for this study. Phillips et al. (1988) were unable to discern differential patterns of variability useful in identification of taxonomic groups; between-groups similarities ranged from 0.925 to 0.992 (Nei [1978] unbiased genetic identity).

Fitts et al. (1992) studied *Purshia subintegra* in Verde Valley, reporting on many important, but heretofore unknown, aspects of the pollination biology of the species. They found that flowers may be pollinated anytime in the first three days after anthesis, the plants are partially self-compatible, and native and introduced bees are primary pollinators. Reciprocal crossing experiments between *P. subintegra* and what was believed to be *P. stansburiana* were also conducted by Fitts et al. (1992). As is discussed in the concluding section of this report, plants from which the *P. stansburiana* was taken are actually introgressed forms.

The purpose of this study was to analyze morphological character variation in species of *Purshia* in order to identify the range of morphological variation in *P. subintegra* and to develop a means of discriminating between *Purshia subintegra*, an endangered species, and other non-endangered *Purshia* taxa with which *P. subintegra* is most likely to be confused. This study was undertaken solely to address the need of natural resource managers to have a means of determining which individuals and populations of *Purshia* are protected under the Endangered Species Act. The methods used in this study were carefully chosen to obtain this result.

METHODS

A total of 216 *Purshia* plants were sampled at 27 widely scattered sites from southeastern to northwestern Arizona for measurement and analysis of morphometric characters (Fig. 1). Much attention was given to sampling *Purshia* in Verde Valley, the only location where it is believed *P. subintegra* and *P. stansburiana* are in close enough proximity that gene exchange might currently be occurring. It was hoped that if hybridization were occurring between the two taxa, it would be possible to isolate characters useful in discriminating between *P. subintegra*, *P. stansburiana*, and the introgressed forms. In determining where to sample, it was important to have some firsthand notion of where the introgressed forms might be: this turned out to be more difficult than it might seem given the disparate views of several researchers. Table 1 lists three separate collection sites for *P. subintegra* in Verde Valley (labeled **D**, **E**, and **F**), in addition to several locations for introgressed forms and one location for *P. stansburiana* on mountains overlooking the valley (Jerome, labeled **X**). Figure 2 shows Verde Valley and collection sites in the valley. The author made three separate collecting trips to Verde Valley—1987, 1989, and 1992—each time expanding the scope of the sampling effort to try to obtain a more representative sample of character variation.

Morphometric samples from each of the 216 sampled plants consisted of two to four 20–40-cm-long branches dried in a standard herbarium press. Samples were collected in April 1987, 1989, and 1992 from each of 4 *P. subintegra* populations, 3 *P. stansburiana* populations, and 20 sites of introgressed forms. Table 1 shows the locations and sample sizes of each collection site. A rigorous stratified-random sampling method was employed at the *P. subintegra* and *P. stansburiana* sites, and at least 10 specimens were collected at each site. Collections at the introgressed form sites were made much more subjectively and the sample sizes were much smaller, only one to six specimens.

Data on 15 characters judged to be potentially useful in taxonomic differentiation between the 27 groups were obtained from the pressed specimens. Floral characters were heavily relied on, and characters that could be used in field identification of unknown specimens were also employed. Table 2 shows the character palette developed for the morphometric analysis. The list of characters indicates that a mix of binary, categorical, and continuous data was used. This was taken into account in subsequent statistical analyses. All measurements and counts were made under a binocular dissecting microscope with a micrometer disk or electronic calipers. Scoring procedures are described in Table 2.

SYSTAT version 4.0 was used to subject the data to more than 50 separate discriminant function analyses (DFA) and principal components analyses (PCA) to identify morphological groups and to determine which characters could be most confidently used to separate the groups. Numerous combinations of characters were used to group like data (binary, categorical, and continuous) and to examine the effects of including ratios as characters (hypanthium-pedicel length/width, sepal length/width, petal length/width) in the data set. Initial analyses using PCA were run on several combinations of characters to identify characters responsible for within-group similarity.

A priori assignments of plants to groups required for DFA involved grouping collection sites in several combinations by morphological, geographical, and ecological criteria. Most DFAs were run with the following groupings: (1) **27-group analysis**, all 27 collection sites coded as separate groups; (2) **3-group analysis**, 4 *P. subintegra* sites, 3 *P. stansburiana* sites, and all introgressed forms in one group; (3) **4-group analysis**, 4 *P. subintegra* sites, 3 *P. stansburiana* sites, and the introgressed forms separated into two groups identified as "Tonto" and "Verde."

RESULTS

Purshia subintegra can be differentiated from *P. stansburiana* and introgressed forms by leaf glandularity and leaf lobing. The mean score of leaf glandularity in *P. subintegra* is less than 0.4, and the mean number of lobes/leaf is 2.5 or less. All others are more glandular or have more leaf lobes. A population of what I initially believed to be introgressed forms at site a (Fig. 2) in Verde Valley possesses glandularity and lobing characteristics of *P. subintegra* and, based on this and the results of the multivariate analyses, should probably be classified as *P. subintegra*.

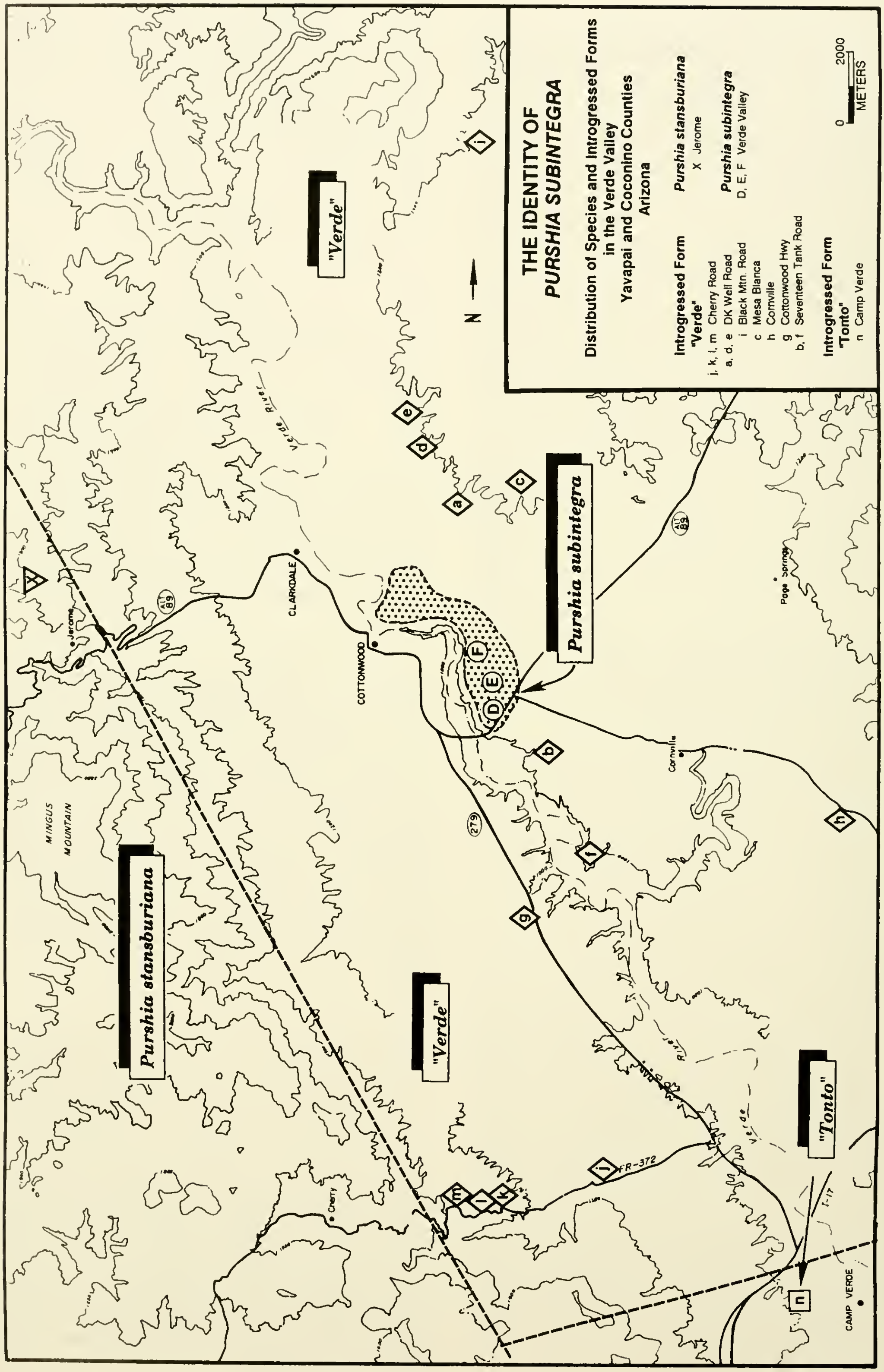

THE IDENTITY OF
PURSHIA SUBINTEGRA
Distribution of Species and Introgressed Forms
in the Verde Valley
Yavapai and Coconino Counties
Arizona
Introgressed Form
"Verde"
j, k, l, m Cherry Road
a, d, e DK Well Road
i Black Mtn. Road
c Mesa Blanca
h Cornville
g Cottonwood Hwy
b, f Seventeen Tank Road
Introgressed Form
"Tonto"
n Camp Verde
Purshia stansburiana
X Jerome
Purshia subintegra
D, E, F Verde Valley
0 2000
METERS
N
"Verde"
"Verde"
"Tonto"
Purshia stansburiana
Purshia subintegra
MINGUS MOUNTAIN
Jerome
CLARKDALE
COTTONWOOD
Cornville
Page Springs
Cherry
CAMP VERDE
Verde River
ALT 89
279
FR-372
I-17

Fig. 2. Distribution of sampling sites, species, and introgressed forms in Verde Valley, Yavapai Co., Arizona.

TABLE 2. Characters measured for analysis of character variation in *Purshia stansburiana*, introgressed forms, and *Purshia subintegra*. Descriptions of the character measurements used in multivariate analyses and acronyms (in parentheses) used as variable labels in Tables 4 and 5. Most hypanthia-pedicel, petal, sepal, pistil, and stamen measurements and counts were from the same five flowers from each plant.

1. **Leaf pubescence.** (LEFPUB) The adaxial surface of *Purshia* leaves is densely tomentose, though the midvein is often bare. The abaxial surface ranges from completely glabrous to completely obscured by long arachnoid hairs. Twenty leaves from each of the 216 plant specimens were scored on an index of leaf pubescence density. Only the dorsal (abaxial) surface was scored. The scale ranged from 1 (completely to nearly completely glabrous) to 5 (densely pubescent).

2. **Leaf glands.** (LEAFGLAN) Ten leaves from each of the 216 plants were examined and scored for presence or absence of impressed-punctate glands.

3. **Hypanthium-pedicel glands.** (HYPGLAN) Five hypanthia (with pedicels) from each plant were examined and scored for presence or absence of stipitate glands.

4. **Leaf lobes.** (LOBES) The number of lobes on each of 20 leaves from each of the 216 plants was counted. The leaf tip was not counted. Lobes varied in distinctness, i.e., from much longer than wide to mere bumps on the edge of the leaf. Even the most minor lobes were scored. Figure 3 illustrates variation in leaf lobing among *P. subintegra*, the "Tonto" and "Verde" introgressed forms, and *P. stansburiana*, and provides an example of lobe scoring.

5–7. **Hypanthium-pedicel dimensions.** (HYPLGTH, HYPWDTH) Length and maximum width of five hypanthia-pedicels from each of the 216 plants were measured under a binocular dissecting microscope using a micrometer disk or electronic calipers. The length/width ratio was also entered as a character variable (HYPRAT).

8–10. **Sepal dimensions.** (SEPLGTH, SEPWDTH) All sepals (usually 5) from five flowers from each of the 216 plants were dissected and measured under a microscope using a micrometer disk or electronic calipers. Maximum (basal) width and length of the sepals were recorded. The length/width ratio was also entered as a character variable (SEPRAT).

11–13. **Petal dimensions.** (PETLGTH, PETWDTH) All petals (usually 5) from five flowers from each of the 216 plants were dissected and measured under a microscope using a micrometer disk or electronic calipers. Maximum width and length of the petals were recorded. The length/width ratio was also entered as a character variable (PETRAT).

14. **Pistil number.** (PSLSFLR) Flowers normally contained 2–4 pistils. Aborted pistils were easily distinguished by their small size (<1.25 mm long) and brown to dark brown color. Viable pistils were pale yellow with silvery-white achene hairs and were nearly always longer than 1.25 mm. The total number of pistils per flower was counted on each of the 216 specimens, as well as the number of viable and aborted pistils.

15. **Number of stamens.** (STMNS) Stamens were counted in five flowers from each of 216 plants.

Table 3 lists mean values and standard errors obtained for each of the 15 characters included in the analysis for each of the four identified groups of *Purshia* spp. Figure 4 illustrates the distribution of variation in sepal and hypanthium-pedicel dimensions. Note that sepal length and width are highly and positively correlated among groups, while hypanthium-pedicel width and length are not. *P. subintegra* plants have shorter, narrower sepals, while *P. stansburiana* have longer, wider sepals; introgressed forms are intermediate. "Tonto" forms have very long, wide hypanthia-pedicels, while "Verde" forms have slightly shorter, but much narrower, hypanthia-pedicels; neither of the two introgressed forms is intermediate in hypanthium-pedicel dimensions between the supposed parent species, *P. subintegra* and *P. stansburiana*.

Principal Components Analysis

Rotated factor scores derived from three PCAs are listed by character in Table 4 and are graphed in Figure 5. The first three factor axes together account for 73–87% of variance in the data. Horizontal relationships on the FACTOR(2)/FACTOR(1) graphs for each analysis (x-axis, Figs. 5A–5C) are primarily based on leaf lobing, while vertical relationships are based on glandularity. The horizontal relationship is again based on glandularity in the FACTOR(3)/FACTOR(2) graphs (y-axis, Figs. 5A–5C), but the vertical relationship (z-axis, Figs. 5A–5C) is mostly influenced by hypanthium-pedicel length.

PCAs illustrate similarities of the three groups of *Purshia* spp. to each other, but graphs must be interpreted carefully. It appears that

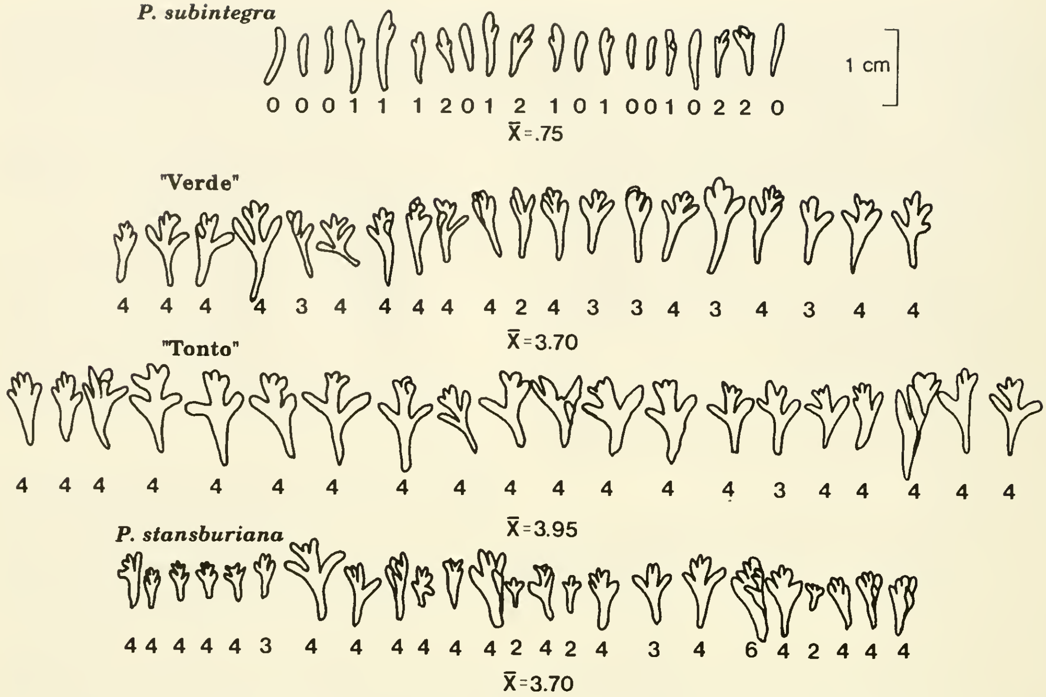


Fig. 3. Variation in leaf lobing and size in *Purshia subintegra*, "Verde" and "Tonto" introgressed forms, and *Purshia stansburiana*. Arrays of 20 leaves scored for pubescence, glandularity, and lobing from typical specimens in each group. Number of leaf lobes scored for each leaf and mean score for each plant are shown.

P. stansburiana groups (**X–Z**) are lost among "Verde" introgressed forms (**b**, **c**, **d**, **e**, **f**, **g**, **h**, **i**, **k**, **l**, **m**), but a careful examination of the distribution of points along FACTOR(3) (z-axis) shows that, primarily on the basis of hypanthium-pedicel length, *P. stansburiana* are more similar to each other. *P. subintegra* and *P. stansburiana* groups (**A–F** and **X–Z**, respectively) are usually closest to each other. Introgressed forms (**a–r**) are more loosely grouped together or near *P. subintegra* or *P. stansburiana*.

Discriminant Function Analysis

Univariate and multivariate F-tests conducted as part of DFA indicated that 14 of 15 characters used were significant at or below the .001 level of significance. Sepal length/width ratio was the only character that did not produce a high F-number. This was true of all character combinations and a priori grouping assumptions.

Two-dimensional graphical illustrations of canonical factor scores often used to show groupings derived from DFA are partially dependent on initial group assignments. For this reason, DFAs were first run on data matrices in which groups were assigned according to the 27 collection sites for each plant, rather than a preconceived notion of the classification of each plant. A series of 27-group analyses were run (Figs. 6A, 6D, 6G) using the 15-, 7-, and 4-character sets. This clearly showed that the data naturally fall into at least three or four groups, depending on how many characters are used.

Results of the 27-group DFAs were used to reclassify each plant into one of three or four groups. Bylas, Burro Creek, Horseshoe Lake, and Verde Valley (sites **D**, **E**, **F**) plants were classified as *P. subintegra*. Plants collected from Jerome, Skull Valley, and Sonoita were placed in *P. stansburiana*. All other plants were placed in "Verde" or "Tonto" introgressed forms, or were combined together in a single group of introgressed forms. Figure 6 illustrates results of nine DFA analyses with three character suites, each analyzed on two additional a priori grouping assumptions.

Character suites containing as few as two characters (e.g., hypanthium-pedicel length

TABLE 3. Characteristics of 27 groups of sampled *Purshia* spp. Mean values and standard errors (in parentheses) are listed for 15 measured characters of 27 sample sites and 216 specimens.

Character	*Purshia subintegra*	"Verde"	"Tonto"	*Purshia stansburiana*
Leaf pubescence	2.075	1.538	1.330	1.393
(scale 1–5)	(0.052)	(0.055)	(0.085)	(0.091)
Leaf lobes	0.721	3.696	3.988	3.734
(count)	(0.074)	(0.135)	(0.109)	(0.083)
Leaf glands	0.020	0.863	0.200	1.000
(presence-absence)	(0.012)	(0.042)	(0.083)	(0.000)
Hypanthium-pedicel glands	0.107	0.891	0.400	1.000
(presence-absence)	(0.028)	(0.046)	(0.112)	(0.000)
Hypanthium-pedicel length	5.098	9.170	10.113	6.620
(mm)	(0.073)	(0.266)	(0.674)	(0.151)
Hypanthium width	2.447	2.154	3.258	2.945
(mm)	(0.033)	(0.039)	(0.115)	(0.071)
Hypanthium-pedicel length/width	2.132	3.591	3.147	2.275
	(0.031)	(0.086)	(0.213)	(0.043)
Sepal length	3.565	4.050	3.961	4.886
(mm)	(0.042)	(0.069)	(0.150)	(0.115)
Sepal width	2.818	3.283	3.498	4.295
(mm)	(0.031)	(0.056)	(0.102)	(0.089)
Sepal length/width	1.282	1.248	1.390	1.151
	(0.014)	(0.018)	(0.126)	(0.022)
Petal length	8.494	9.880	10.678	11.246
(mm)	(0.109)	(0.164)	(0.342)	(0.215)
Petal width	5.730	8.357	8.289	10.307
(mm)	(0.087)	(0.219)	(0.305)	(0.288)
Petal length/width	1.536	1.226	1.311	1.147
	(0.201)	(0.027)	(0.024)	(0.022)
Stamens	48.582	67.404	66.585	88.961
(count)	(0.879)	(1.760)	(3.245)	(4.035)
Pistils	3.465	5.364	5.222	5.486
(count)	(5.364)	(0.088)	(0.204)	(0.179)

and sepal width), and essentially all other combinations of characters up to the full 15 available, consistently produced the same pattern: *P. subintegra* and *P. stansburiana* are grouped in distinct clusters, but the *P. subintegra* cluster is normally much more cohesive than the other, while both introgressed forms are usually loosely grouped in one or two clusters.

The best discrimination between groups was obtained using all 15 characters, with a 3-group assumption (Fig. 6B). There is virtually no overlap between groups, except in the case of collection site a. Table 5 lists canonical loadings for each character on each discriminant function (DF) obtained from DFA. These are useful in identifying the characters most responsible for discriminating on each of the DFs. In every DFA, leaf glandularity and lobing are the highest loading characters on DF I, and frequently load highest on the second and third DFs as well. In the 15- and 7-character suite DFAs, hypanthium-pedicel length is usually the third highest loading character.

More tightly clustered DFA plots of *P. subintegra* are taken to indicate less morphological variability in these four populations relative to the other groups. Separate DFAs and PCAs run only on the *P. subintegra* plants indicate that significant variability occurs within this group, and post-hoc identification of each plant into one of the four *P. subintegra* groups is about 50–90% accurate. In contrast, DFAs using only *P. stansburiana* and introgressed forms (i.e., no *P. subintegra*) provided poor discrimination between those groups.

Each DFA produced a set of group membership probabilities for each plant. These were used to create the tables of a priori and predicted memberships shown in Table 6. These predictions were almost always highly accurate, over 95%. In the 4-character, 4-group analysis (Table 6), DFA was only about 80% accurate for the "Verde" and "Tonto" groups, but over 95% accurate for identifying *P. subintegra* and *P. stansburiana*.

"Tonto" plants have long hypanthia-pedicels (mean 10.1 mm) and eglandular leaves, while

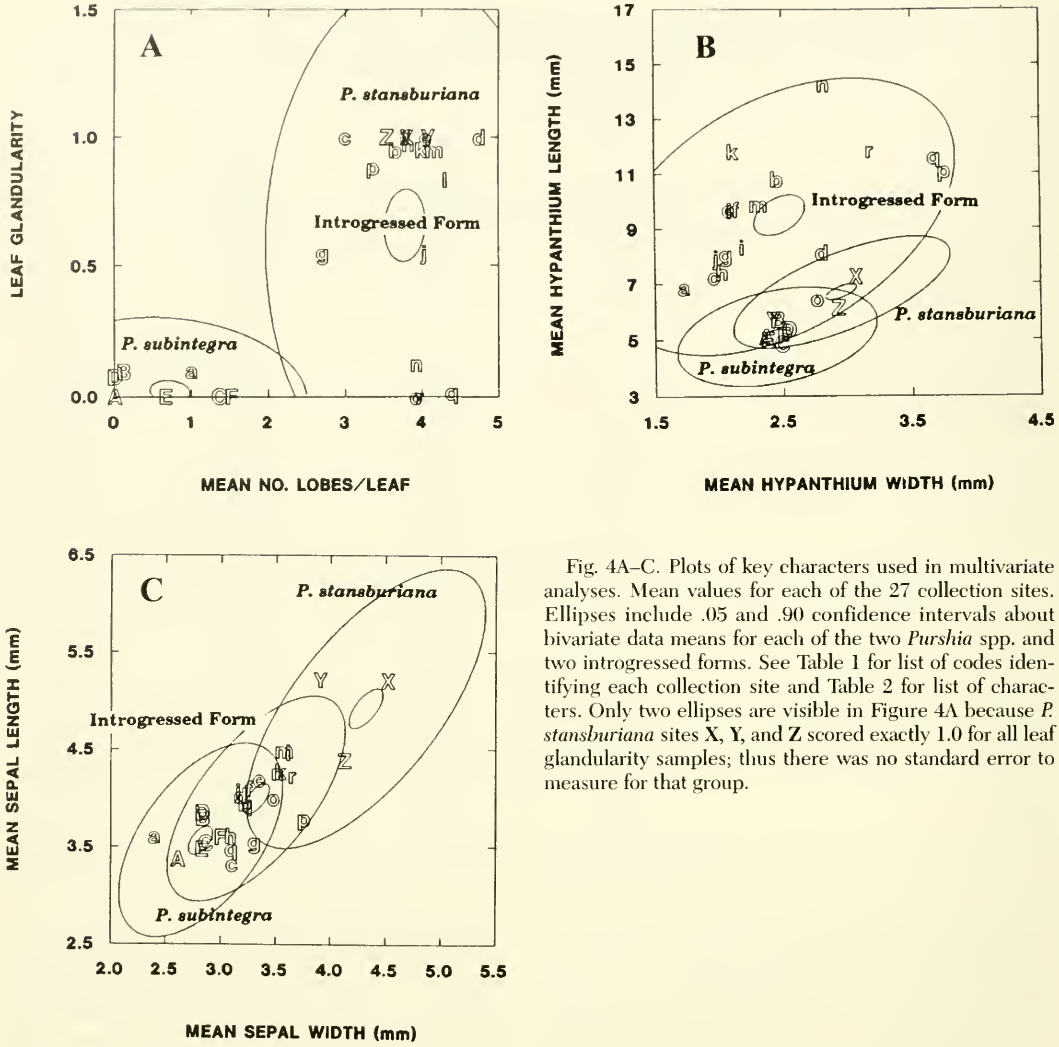


Fig. 4A–C. Plots of key characters used in multivariate analyses. Mean values for each of the 27 collection sites. Ellipses include .05 and .90 confidence intervals about bivariate data means for each of the two *Purshia* spp. and two introgressed forms. See Table 1 for list of codes identifying each collection site and Table 2 for list of characters. Only two ellipses are visible in Figure 4A because *P. stansburiana* sites X, Y, and Z scored exactly 1.0 for all leaf glandularity samples; thus there was no standard error to measure for that group.

"Verde" plants have slightly shorter hypanthia-pedicels (mean 9.2 mm) and glandular-punctate leaves. Generally, "Tonto" plants are found in Gila County, Arizona, on lakebed deposits around Roosevelt Lake in Tonto Creek basin. Note that Camp Verde, site **n**, is included in the "Tonto" introgressed form despite its location in Verde Valley in close proximity to the "Verde" introgressed form. This assignment resulted from inspection of previous DFAs and PCAs. Pinal Creek "Tonto" plants (site **p**) are frequently given the highest probability of belonging to the "Verde" introgressed form despite their location far away from any other "Verde" collection site (Fig. 2). Plants at these collection sites illustrate the high degree of variability in phenotypic expression of introgressed forms.

DISCUSSION

Multivariate analysis of character variation clearly indicates that the four *Purshia subintegra* populations sampled exhibit a coherent syndrome of characters. Although there is some variation between populations, the taxonomy developed by Schaack (1987b) is not supported by the analyses. Specimens claimed to be of hybrid origin by Schaack (1987a, 1987b) from among the type material collected at Burro Creek should be considered to represent *P. subintegra*. It may be speculated that leaf lobing and leaf and hypanthium-pedicel glandularity exhibited by these specimens arose from a limited exchange of genetic information with *P. stansburiana* during a period of brief proximity in the ranges of the two species.

TABLE 4. Principal components analysis of *Purshia* spp. showing factor axis loadings resulting from analysis of the full set of measured characters and two abbreviated sets. Scores from the first three factor axes are given for each character set.

15-character set	Factor axis		
	1	2	3
LOBES	0.557	0.212	0.221
STMNS	0.118	0.111	0.045
PETWDTH	0.092	0.107	0.075
PSLSFLR	0.074	0.088	0.101
SEPWDTH	0.041	0.059	0.017
PETLGTH	0.021	0.043	0.056
SEPLGTH	0.010	0.045	0.025
LEAFGLAN	0.085	0.259	0.103
HYPLGTH	0.054	0.050	0.256
HYPWDTH	0.010	–0.016	–0.007
HYPGLAN	0.076	0.304	0.090
PETRAT	–0.050	–0.040	–0.015
SEPRAT	–0.013	–0.019	0.004
LEFPUB	–0.057	–0.072	–0.063
HYPRAT	0.024	0.035	0.188
% of total variance	32.432	22.723	17.367
7-character set			
LOBES	0.569	0.252	0.185
SEPWDTH	0.044	0.067	0.013
SEPLGTH	0.015	0.055	0.015
HYPWDTH	0.006	–0.014	0.018
LEAFGLAN	0.086	0.274	0.073
HYPLGTH	0.066	0.081	0.257
HYPGLAN	0.077	0.316	0.069
% of total variance	43.075	31.713	13.894
4-character set			
LOBES	0.590	0.177	0.197
LEAFGLAN	0.101	0.166	0.084
HYPGLAN	0.091	0.302	0.074
HYPLGTH	0.075	0.057	0.263
% of total variance	50.081	20.615	16.208

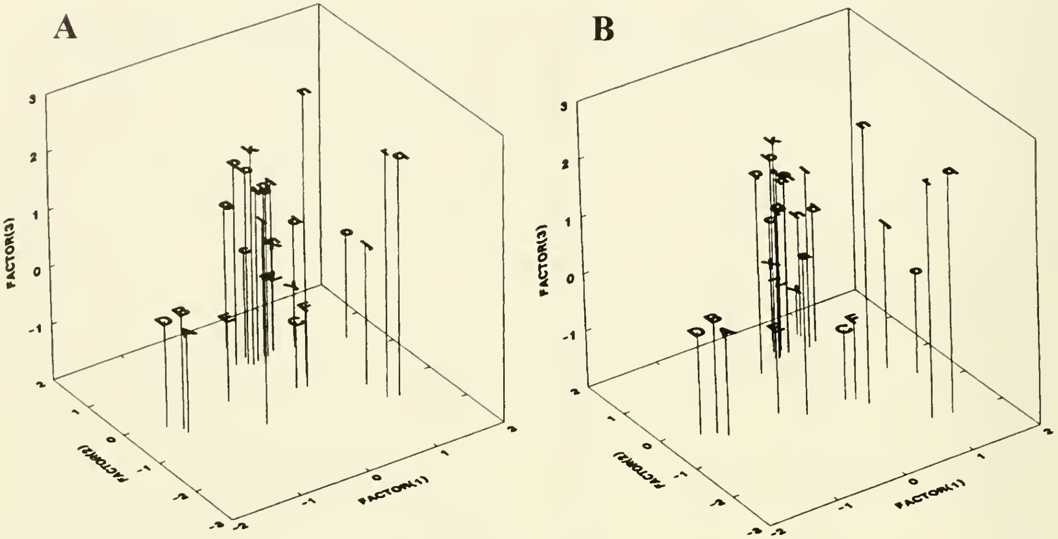
Whatever gene exchange occurred must have occurred many generations ago and did not sufficiently influence the values taken by Burro Creek *Purshia* plants in respect to the 15 characteristics evaluated here to differentiate these specimens from *P. pinkavae* represented by the specimens I collected at Bylas.

Anderson (1986) reported that the Horseshoe Lake population primarily comprised hybrid and introgressed forms that were in the process of being “swamped out” by *P. stansburiana*. It is now clear that all *Purshia* plants in the area are appropriately identified as *P. subintegra* and that *P. stansburiana* is not present except perhaps at higher elevations several kilometers distant.

At Bylas, Burro Creek, and Horseshoe Lake, *P. subintegra* is unlikely to exchange genetic information with any other *Purshia* taxon. *P. subintegra* in Verde Valley is restricted to a band roughly 1 km wide and 6 km long, paralleling the Verde River east of Cottonwood, Arizona, which may extend north along a series of bluffs overlooking Verde Valley (collection site **a**). This isolated edaphic relict is surrounded by pockets of *Purshia* plants that appear to be intermediate in some characters between it and *P. stansburiana*, which occurs only at elevations above 1500 m. Table 7 presents a simplified chart of ecological and morphological characteristics that may be used to distinguish *P. subintegra*, introgressed forms, and *P. stansburiana*. Generally, *P. subintegra* plants have no leaf glands, 0–2 lobes per leaf, and hypanthia-pedicels about 5 mm long; *P. stansburiana* plants have abundant leaf glands, at least 3–4 lobes per leaf, and hypanthia-pedicels about 6.6 mm long; introgressed forms leaves are glandular or not, have at least 3–4 lobes per leaf and hypanthia-pedicels about 9–10 mm long. Approximately 86% of leaves of “Verde” forms are glandular, while only 20% of “Tonto” leaves are glandular.

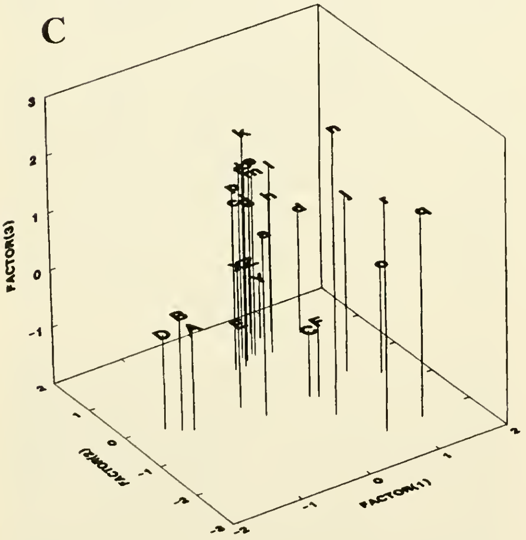
“Verde” and “Tonto” plants are rare to uncommon throughout the Verde and Salt River basins between 600 and 1500 m elevation. In Verde Valley, “Verde” plants are found on the same Verde Formation soils as support *Purshia subintegra*. Collection site **i**, of “Verde” plants from Verde Valley, occurs on sandy reddish soils derived from weathered Supai Formation sandstones. Some of the “Tonto” collection sites occurred on Quaternary alluvium derived from weathered granites and schists, some occurred on limy soils derived from Tertiary lakebed deposits, and some on conglomerates composed of volcanic ashes and mudflows. Most of these sites were characterized by sparsely vegetated sterile or poor soils.

Fitts et al. (1992) attempted to perform reciprocal crossing experiments involving *P. subintegra* and *P. stansburiana* with pollen from what the investigators believed to be *P. stansburiana* in a dry wash only a few score meters from their *P. subintegra* study subjects at Dead Horse Ranch State Park (about 2 km north of Cottonwood), and approximately 3 km northwest of Verde Valley *P. subintegra* sites **D**, **E**, and **F** (Fig. 2). Reciprocal crosses resulted in 50% seed set, compared with 80% for within-species outcrossed flowers and 20% for



15 CHARACTER SET

7 CHARACTER SET



4 CHARACTER SET

Fig. 5A–C. Three-dimensional plots of mean factor scores for each of the 27 collection sites of *Purshia* spp. and introgressed forms included in the PCA on the first three factor axes. See Table 1 for locations and descriptions of sites corresponding to letter codes and Table 4 for lists of characters used in the three sets.

self-pollinated flowers. Seeds appeared normal and viable, although no attempt has been made to study viability of the seeds produced from reciprocal crosses (V. Tepedino personal communication June 1992).

Identity of the plants from which *P. subintegra* pollen was taken is clear, but the question remains whether reciprocal crossing experiments were conducted with pollen from *P. stansburiana* or "Verde" introgressed forms. U.S. Fish and Wildlife Service botanists Sue Rutman and Bruce Palmer collected four post-reproductive specimens of *Purshia* sp. in November 1992 from the same dry wash used by Fitts et al. in

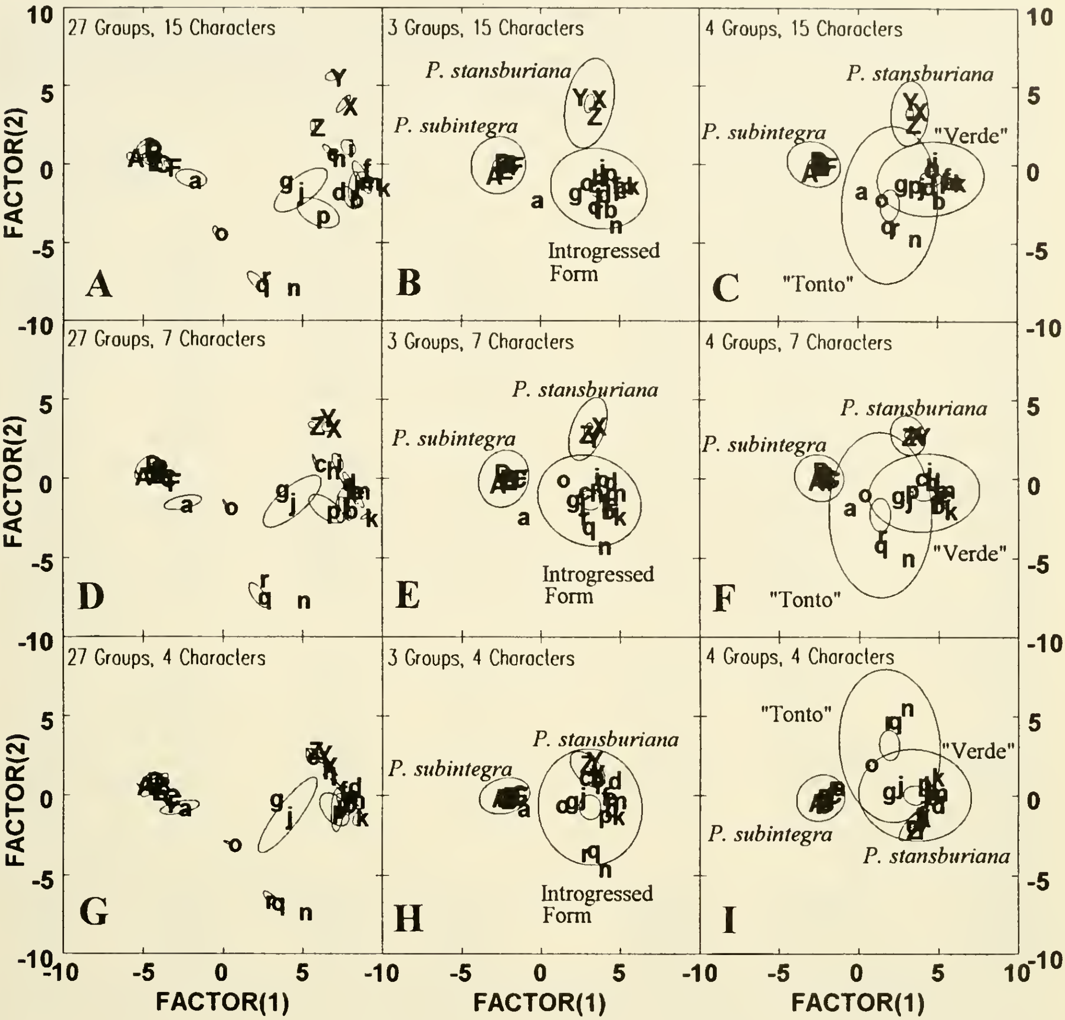


Fig. 6A–I. Plots of mean factor scores for each of the 27 collection sites of *Purshia* spp. and introgressed forms included in nine separate DFAs on the first two discriminant functions. Ellipses representing .90 confidence intervals about bivariate data means for each of the 27-group analyses (A, D, G), and .90 and .05 confidence interval ellipses for the 3- (B, E, H), and 4- (C–I) groups of *Purshia* spp. and introgressed forms.

their pollination studies. Like Fitts et al., Rutman and Palmer identified these specimens as *P. stansburiana*, based primarily on glandularity and leaf lobing. As already stated, I believe there is no *P. stansburiana* in Verde Valley; the species is restricted to elevations over 1500 m. The four pressed specimens were rehydrated and meaningful data were obtained from hypanthia-pedicels that were dried but persisted in place. Two of the specimens had one or two fresh flowers in anthesis. Data collected from these specimens—including leaf glandularity, leaf lobing, hypanthium glandularity, hypanthium length, hypanthium width, sepal length, and sepal width—were added to the data set used for previous analyses. The four new specimens were classified through DFA as *P. stansburiana* or the "Verde" introgressed form, but not as *P. subintegra* or the "Tonto" introgressed form, depending on which a priori grouping assumptions were used. When the four new specimens were placed in their own group and added to the 27-group analysis discussed above, they were easily distinguished from *P. stansburiana* and placed in the "Tonto" introgressed form group, primarily based on hypanthium dimensions.

Whether Fitts et al. (1992) used *P. stansburiana* or plants more representative of what should be called an 'introgressed form', their

TABLE 5. Canonical within-groups structures obtained by discriminant function analysis of *Purshia* spp. Canonical loadings resulting from analysis of the full set of measured characters and two abbreviated sets. Each character set is subjected to analysis under three a priori grouping assumptions: 27 groups (one for each specimen collection site), 3 groups (*Purshia subintegra*, introgressed forms, *P. stansburiana*), 4 groups (*P. subintegra*, introgressed form "Verde," introgressed form "Tonto," *P. stansburiana*).

15-character set	27-group analysis		3-group analysis		4-group analysis	
DF	1	2	1	2	1	2
LEAFGLAN	0.594	0.444	0.457	0.294	0.609	0.494
HYPGLAN	0.256	0.145	0.338	0.180	0.360	0.233
LEFPUB	–0.101	0.078	–0.196	–0.040	–0.175	–0.008
LOBES	0.500	–0.300	0.632	0.061	0.579	–0.043
HYPLGTH	0.309	–0.552	0.411	–0.314	0.374	–0.439
HYPWDTH	0.030	–0.090	0.057	0.199	0.019	0.094
HYPRAT	0.234	–0.400	0.336	–0.406	0.330	–0.444
SEPLGTH	0.154	0.202	0.225	0.373	0.207	0.341
SEPWDTH	0.224	0.198	0.340	0.532	0.299	0.455
SEPRAT	–0.045	–0.056	–0.037	–0.117	–0.040	–0.131
PETLGTH	0.159	0.021	0.255	0.210	0.228	0.145
PETWDTH	0.281	0.107	0.428	0.375	0.388	0.315
PETRAT	–0.158	0.001	–0.251	–0.122	–0.240	–0.119
PSLSFLR	0.272	–0.059	0.439	0.106	0.408	0.048
STMNS	0.264	0.176	0.318	0.385	0.288	0.335
7-character set						
LEAFGLAN	0.639	0.531	0.533	0.304	0.690	0.498
HYPGLAN	0.276	0.201	0.392	0.180	0.406	0.226
LOBES	0.545	–0.249	0.726	0.003	0.637	–0.118
HYPLGTH	0.341	–0.633	0.461	–0.425	0.403	–0.551
HYPWDTH	0.036	–0.068	0.071	0.234	0.015	0.107
SEPLGTH	0.164	0.229	0.269	0.425	0.235	0.369
SEPWDTH	0.241	0.267	0.406	0.604	0.337	0.490
4-character set						
LEAFGLAN	0.651	0.720	0.534	0.602	0.719	–0.612
HYPGLAN	0.281	0.255	0.394	0.358	0.426	–0.260
LOBES	0.565	–0.362	0.730	0.032	0.685	0.289
HYPLGTH	0.357	–0.641	0.466	–0.796	0.425	0.621

experiment indicated a significant potential for gene exchange outside of *P. subintegra*.

The introgressed forms, "Verde" and "Tonto," are nearly identical to *P. stansburiana* in leaf lobing, leaf vestiture, stature, and number of pistils per flower. They are only intermediate in leaf and hypanthium-pedicel glandularity, sepal and petal dimensions, and number of stamens per flower. Length and width of the hypanthium-pedicel in the introgressed forms are not intermediate between *P. subintegra* and *P. stansburiana*; hypanthia are consistently longer and, for most populations, narrower. Introgressed forms do not appear to be closer to *P. subintegra* in any of the scored or measured characters. Cooperrider (1957) and Anderson and Harrison (1979) studied a similar situation in *Quercus marilandica*, *Q. velutina*, and a putative hybrid. Anderson and Harrison (1979) used morphological data and PCA to test Cooperrider's (1957) use of Anderson's (1949) hybrid index to determine the degree of introgression between putative hybrid and putative parent species in Iowa. Data collected by Anderson and Harrison in Oklahoma showed that, in some characters, the hybrid was definitely intermediate, while in other characters the hybrid was more similar to *Q. velutina* than *Q. marilandica*. Ordinations of data in PCA showed putative hybrids were clearly more similar to *Q. velutina*. On the surface one would expect that putative hybrids are backcrossing with *Q. velutina*, but not with *Q. marilandica*. Anderson and Harrison, pointing out that they can find no ecological reason why backcrosses with *Q. marilandica* should

TABLE 6. Post-hoc classification of cases in groups from discriminant function analysis. A priori classifications are on the left side, predicted group memberships on the top.

216 cases, 15 characters, 3 groups

Actual group	*P. stansburiana*	Introgressed form	*P. subintegra*	Total
P. stansburiana	29	0	0	29
Introgressed form	1	62	2	65
P. subintegra	0	0	122	122
Total	30	62	124	216

216 cases, 15 characters, 4 groups

Actual group	*P. stansburiana*	"Verde"	"Tonto"	*P. subintegra*	Total
P. stansburiana	28	0	0	0	28
"Verde"	0	44	0	2	46
"Tonto"	1	0	19	0	20
P. subintegra	0	0	0	122	122
Total	29	43	19	124	216

216 cases, 4 characters, 3 groups

Actual group	*P. stansburiana*	Introgressed form	*P. subintegra*	Total
P. stansburiana	29	0	0	29
Introgressed form	13	49	3	65
P. subintegra	0	0	122	122
Total	42	49	125	216

216 cases, 4 characters, 4 groups

Actual group	*P. stansburiana*	"Verde"	"Tonto"	*P. subintegra*	Total
P. stansburiana	28	0	0	0	28
"Verde"	9	32	2	3	46
"Tonto"	0	4	16	0	20
P. subintegra	2	0	0	120	122
Total	39	36	18	123	216

not be just as prevalent as those with *Q. velutina*, argue instead that the problem lies in not properly delineating the range of variation in putative parents, putative hybrids, and introgressed forms. They found characters with non-intermediate dimensions, but in every case these were closer to one putative parent than the other and not, as described here for hypanthium-pedicel dimensions, quite different from both putative parents. This could be accounted for by several factors including natural variation, heterosis, and linked gene controls of simple characters. No breeding experiments involving *P. subintegra* and *P. stansburiana* have yet been carried out so that we may describe the quantitative characteristics of an actual hybrid. It has only been assumed so far that a hybrid should possess a morphology roughly intermediate between the parents. The close proximity of some "Verde" plants to *P. subintegra* suggests the opportunity for hybridization exists now, although data presented here do not indicate which of the sampled plants, if any, represent F_1 hybrids.

Results obtained in this study of *Purshia* indicate that while it is reasonably simple to determine what is *P. subintegra*, it is not always possible to distinguish what have been referred to as 'introgressed forms' from *P. stansburiana*. Results of Anderson and Harrison (1979), in a situation similar to that described here, might suggest that we consider introgressed forms a part of the natural variation inherent in locally adapted *P. stansburiana* genomes, and not, as has been assumed by many, a result from a predominance of backcrosses with *P. stansburiana*. Why then are forms as similar to *P. stansburiana,* as described above, found in such proximity to *P. subintegra* at Dead Horse Ranch, and how is it that *P. subintegra* in Verde Valley has remained morphologically distinct despite what appears to be ample opportunity for extensive hybridization?

TABLE 7. Reliable characters useful in discriminating between *P. subintegra*, *P. stansburiana*, and introgressed forms. Quantities in parentheses are mean values taken from Table 3. Other data are based on author's observations and Anderson (1986).

Character	*Purshia subintegra*	"Verde"	"Tonto"	*Purshia stansburiana*
Distribution	640–1065 m elevation, northwest of Bylas, Graham Co.; north of Burro Cr., Mohave Co.; Horseshoe L., Maricopa and Yavapai cos.; east of Cottonwood, Yavapai Co.	1020–1385 m elevation, Verde Valley, Yavapai Co.	725–1015 m elevation, near Camp Verde, Yavapai Co.; Tonto Basin and south of Globe, Gila Co.	Statewide (except southwestern quarter), generally above 1500 m elevation
Ecology	Restricted to limey soils derived from weathered Tertiary lakebed limestones	Mostly restricted to limey soils derived from weathered Tertiary lakebed limestones, occasionally on Supai Formation sandstones	Limey soils of weathered lakebed limestones; other limestone formations, soils derived from volcanics and alluvial materials	Various
Growth form	Shrub, up to 1 m tall, stems widely and sparingly branching from the base	Shrub, 1–2 m tall when mature, widely and sparingly branched from the base	Shrub, 1–2, or sometimes 3 m tall when mature, widely and sparingly branched from the base	Shrub, 3–5 m tall when mature, stems erect, branching from the base
Leaf shape	Entire or 1–2 lobes (0.7 lobes per leaf)	3–5 lobes (3.7 lobes per leaf	3–5 lobes (4.0 lobes per leaf)	3–5 lobes (3.7 lobes per leaf)
Leaf vestiture	Very densely pubescent on lower surface, less pubescent on upper surface	Very densely pubescent on lower surface, less pubescent to bare on upper surface	Very densely pubescent on lower surface, less pubescent to bare on upper surface	Very densely pubescent on lower surface, less pubescent to bare on upper surface
Leaf glandularity	Usually none, rarely with impressed punctate glands (2% glandular)	Usually glandular (86% glandular)	Usually not glandular (20% glandular)	Abundantly glandular (100% glandular)
Hypanthia-pedicels	Short, usually not glandular, rarely with stalked glands (5.1 mm long, 2.4 mm wide, 11% glandular)	Long, usually with stalked glands (9.2 mm long, 2.2 mm wide, 89% glandular)	Long, usually without stalked glands (10.1 mm long, 3.2 mm wide, 40% glandular)	Short, with abundant stalked glands (6.6 mm long, 2.9 mm wide, 100% glandular)
Sepals	Short and narrow (3.6 mm long, 2.8 mm wide)	Long and narrow (4.1 mm long, 3.3 mm wide)	Short and wide (4.0 mm long, 3.5 mm wide)	Long and wide (4.9 mm long, 4.3 mm wide)
Petals	Short and very narrow (8.5 mm long, 5.7 mm wide)	Long and wide (9.9 mm long, 8.4 mm wide)	Long and wide (10.7 mm long, 8.2 mm wide)	Very long and very wide (11.3 mm long, 10.3 mm wide)
Pistils	3–4 (3.5 per flower)	4–6 (5.4 per flower)	4–6 (5.2 per flower)	4–6 (5.5 per flower)
Stamens	(48.6 per flower)	(67.4 per flower)	(66.6 per flower)	(89.0 per flower)

Deciding whether the introgressed forms, "Verde" and "Tonto," should be considered as such, or, alternatively as manifestations of a broader concept of *P. stansburiana*, is not vital to the need that prompted this study: namely, a means of accurately identifying *P. subintegra* for the purpose of determining what is and is not to be considered endangered under federal law.

No nomenclatural revisions or additions to the classification of *Purshia* are proposed; plants reported here as introgressed forms should be regarded as such unless carefully controlled crossing and backcrossing experiments are conducted that clearly show resulting progeny are essentially identical to "Verde" and "Tonto" plants in the field. I recommended in 1986 that most fruitful results for the interpretation of morphological variation in *P. subintegra* would be obtained from a 'common garden' experiment. Under more carefully controlled conditions than may be found in the field, it should be possible to trace genetic bases for morphological characters relied on so heavily in this paper. Had such a study been initiated at that time, we may very well be enjoying the lucidity provided by early results.

Hybrid formulae for nothotaxa have not yet been validly published for the introgressed forms and should not be until their origins are firmly established. Protective measures of the Endangered Species Act should be applied to those forms that conform to the *P. subintegra* character list in Table 7, but not to plants conforming to the characteristics listed for the introgressed forms or to *P. stansburiana*.

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OBSERVATIONS ON DOUBLE-CRESTED CORMORANTS (*PHALACROCORAX AURITUS*) AT SPORTFISHING WATERS IN SOUTHWESTERN UTAH

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ABSTRACT.—Counts of Double-crested Cormorants (*Phalacrocorax auritus*) were made at 13 reservoirs and lakes in southwestern Utah during 1989–91 to determine current abundance of that species. Food habits of cormorants were studied at three of the reservoirs in 1989. Data were also collected on trout abundance during standardized gill-netting to make comparisons between cormorant numbers and trout abundance. Cormorants were observed at all waters studied except one and were generally most numerous during the spring as they migrated through the area. Estimated cormorant abundance ranged from 0 to 34 bird-days per ha and was highest at the larger, lower-elevation reservoirs. Cormorants were summer residents at several of the larger reservoirs and nested successfully at Piute Reservoir. Trout accounted for 24–81% of the diet of cormorants, with Utah chubs constituting most of the remainder of the diet. Estimates of the annual consumption of fish by cormorants ranged from 0 to 15.8 kg per ha. The index of trout abundance was inversely related to cormorant abundance ($P < .01$) at the waters studied. Cormorants apparently have increased in numbers and extended their range in southwestern Utah during the past decade. This change may be the result of factors that have led to similar changes throughout North America as well as some factors unique to Utah. Methods to mitigate the impact of predation by piscivorous birds on sportfisheries are discussed. The Utah Division of Wildlife Resources has initiated a new management plan at Minersville Reservoir that incorporates piscivorous birds into sportfish management at that reservoir.

Key words: cormorants, Phalacrocorax auritus, *trout, abundance, food habits, predation, management, sport fishing, reservoirs, Utah.*

Various factors influencing survival of stocked trout were examined at Minersville Reservoir, Utah, in 1985–88 (Hepworth and Duffield 1991, Wasowicz 1991). During that study we observed an increase in the number of Double-crested Cormorants (*Phalacrocorax auritus,* hereafter referred to as cormorants) at Minersville Reservoir compared with previous years. An apparent increase in the abundance of cormorants at several other reservoirs was also noted, and we received reports of cormorants at some waters where they previously had not been reported (Walters and Sorenson 1983). Apparent changes in abundance and distribution of this species in Utah coincided with reported increases in the number of cormorants in many parts of North America (Price and Weseloh 1986, Christie et al. 1987, Campo et al. 1988, Findholt 1988). As the relative abundance of cormorants has increased, there have been conflicting reports concerning their impact on recreational fisheries. A number of authors have concluded that cormorants take considerable numbers of game fish and potentially impact important fisheries (Ayles et al. 1976, Myers and Peterka 1976, Christie et al. 1987, Campo et al. 1988). Others have felt that cormorants have had little impact on economically valuable species of fish (Baillie 1947, Carroll 1988, Findholt 1988). To evaluate the potential impact of cormorants on fisheries in southwestern Utah, we continued to document the number of cormorants at Minersville Reservoir and 12 additional waters. We also collected data on trout abundance at these waters during standardized annual gill-netting and initiated a study of the food habits of cormorants at three of the larger reservoirs. Based on these observations, we determined current abundance of cormorants at local waters, compared estimates of cormorant abundance to indices of trout abundance, and estimated annual consumption of fish by cormorants.

STUDY AREA

Data on distribution, relative abundance, and seasonal occurrence of cormorants were collected at 13 reservoirs in southwestern Utah (Table 1). Reservoirs ranged in size from 36 to 1020 ha, and elevations from 910 to 2695 m above MSL. Most reservoirs were originally constructed for irrigation storage and have water levels that fluctuate substantially on an annual basis. Highest water levels occurred in late winter and spring, with minimum levels in the fall following the irrigation season. Fish Lake and Panguitch Lake are natural lakes where storage has been increased by the addition of small dams. All the reservoirs except Quail Creek and Gunlock had ice cover for a period of 2–5 months during winter and spring.

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Sportfishing is a major activity at all of the waters since they are open year-round to angling by the general public with various restrictions (State of Utah 1992). Sportfisheries at all reservoirs except Gunlock are managed, at least in part, as put-grow-and-take trout fisheries. Various sizes and numbers of rainbow trout (*Oncorhynchus mykiss*) were stocked annually at the different reservoirs. Fingerling rainbow (76 mm total length [TL]) were stocked at waters where numbers of competing species were low and predation was not a concern. Larger rainbow (127–178 mm TL) were stocked at reservoirs where survival of small trout was poor because of competition with nongame species and/or predation. Limited numbers of other species of trout were stocked at some waters to provide variety in fishing opportunity. Recruitment from spawning in tributaries associated with reservoirs also provided a small number of trout in addition to those stocked at some of the study waters. Stocked trout were harvested by anglers after they reached a catchable size (>230 mm TL), generally after they had been in the reservoirs for 7–11 months. Few rainbow trout survive longer than 2 years following stocking (Stuber et al. 1985, Hume and Tsumura 1992). Most reservoirs contained few fish species other than trout, and five contained primarily stocked trout (Enterprise, Kolob, Koosharem, Lower Bowns, and Newcastle). Three of the reservoirs contained only stocked trout and Utah chubs (*Gila atraria*; Minersville, Otter Creek, and Panguitch). Two were primarily warm-water fisheries where trout abundance was not evaluated (Gunlock and Quail Creek). The remaining three waters (Fish Lake, Johnson and Piute reservoirs) contained more than two other fish species besides trout. Only two or three of these other species were abundant, while the rest were of minor occurrence.

A number of the waters in which Utah chubs and Utah suckers (*Catastomus ardens*) occurred were periodically treated with rotenone to remove all fish when those nongame species became abundant. When reclamation projects were conducted, chubs and suckers often outnumbered trout by hundreds to one. Following treatments, trout were the

TABLE 1. Description of waters in southwestern Utah where scheduled counts of Double-crested Cormorants were conducted, 1989-91.

Water	Location	Elevation (m)	Maximum surface area (ha)	Fish species present[a]	
				Common	Uncommon
Enterprise Reservoir	T38S R18W, Washington Co.	1755	200	RT	
Fish Lake	T26S R2E, Sevier Co.	2695	1012	RT, LT, SP, US, UC, YP	RS, MS
Gunlock Reservoir	T40S R17W, Washington Co.	1092	108	CC, LB, GS	BC, BG
Johnson Reservoir	T25S R2E, Sevier Co.	2688	285	RT, CT, UC, US	YP, RS
Kolob Reservoir	T38S R11W, Washington Co.	2474	136	RT, CT, BK	
Koosharem Reservoir	T25S R1E, Sevier Co.	2132	125	RT, CT, BK	
Lower Bowns Reservoir	T31S R6E, Garfield Co.	2271	36	RT, CT, BK	
Minersville Reservoir	T29S R8W, Beaver Co.	1677	401	RT, CT, UC	BN
Newcastle Reservoir	T36S R15W, Iron Co.	1659	66	RT	SB
Otter Creek Reservoir	T29S R2W, Piute Co.	1942	1020	RT, UC	CT, BN
Panguitch Lake	T35S, R7W, Garfield Co.	2502	505	RT, BK, BN, CT, UC	
Piute Reservoir	T28S, R2W, Piute Co.	1828	1015	RT, UC, US	BN, CT, RS, SB
Quail Creek Reservoir	T42S, R14W, Washington Co.	910	239	RT, LB, BC, BG	BB

[a] Fish species: RT = rainbow trout, GS = green sunfish, LT = lake trout, SP = splake trout, US = Utah sucker, UC = Utah chub, YP = yellow perch, MS = mottled sculpin, CC = channel catfish, LB = largemouth bass, BC = black crappie, BG = bluegill, CT = cutthroat trout, BK = brook trout, RS = redside shiner, BN = brown trout, SB = smallmouth bass, BB = black bullhead.

predominant species for at least a year or two. In situations where undesirable nongame species of fish could not be completely removed from a drainage, Utah chubs and Utah suckers would gradually increase and eventually return to pre-reclamation densities.

In addition to cormorants, other piscivorous birds observed at the study waters included Common Loons (*Gavia immer*), Western Grebes (*Aechmophorous occidentalis*), American White Pelicans (*Pelecanus erthrorychos*), Mergansers (*Mergus merganser* and *M. serrator*), and Great Blue Herons (*Ardea herodias treganzai*).

METHODS

Counts of cormorants were made at 1- to 3-week intervals at 11 reservoirs during 1989. In 1990 we made biweekly counts at four of the larger reservoirs. Counts were made again in 1991 at the four reservoirs surveyed in 1990, as well as three additional ones. Counts generally began following ice-out at each reservoir and continued through November at most waters. We discontinued counts early at several reservoirs that were drained during the summer or chemically treated to remove nongame fish. At most locations counts were made from shore using binoculars or a spotting scope. At larger reservoirs we often used a boat to facilitate counting. Technicians making counts were instructed using a standard training program by the authors. The same one or two technicians counted birds at all waters during any one year of the study. Cormorants were easily identified. Knowledge of the birds' feeding and resting patterns, as well as other behaviors, also aided in making accurate counts.

An annual estimate of cormorant abundance (bird-days per ha per year) was made for each reservoir studied. The estimate of abundance was calculated using methods commonly employed to estimate sportfishing pressure in creel surveys of anglers (Robson 1960, Lambou 1961). A bird-day was defined as one day spent by one cormorant at a given water. The sampling period was stratified by 3-month intervals, March–May, June–August, and September–November. The number of days within a stratum varied among waters, depending on the time of ice-out and whether a given reservoir was drained or treated in the fall. The number of bird-days for a stratum at a given water was estimated using the following formula:

$$D = K\left(\frac{\sum x_i}{n}\right)$$

$$Var\ (D) = \frac{K^2\left(\sum x_i^2 - \frac{N^2}{n}\right)}{(n-1)\ n}$$

where:

D = estimated total bird-days;
K = number of days within a sampling stratum;
x_i = number of cormorants counted on the i^{th} day;
n = number of days sampled within a stratum;
Var = estimated variance;
N = total cormorants counted per stratum.

$$95\%\ \text{confidence interval} = \pm\ 2\sqrt{Var\ (D)}.$$

The estimate of annual cormorant abundance was the sum of estimated bird-days for strata within a sampling year divided by the mean surface area of the reservoir.

Gill-nets were used to estimate trout abundance at each reservoir (Bennett 1962, Hubert 1983) during early spring, 2–4 weeks after winter ice cover was completely gone. Net numbers, styles, and locations were based on long sampling histories at each water. Gill-net data have been collected on most of the study waters for 10 years or more. We followed standardized netting practices used by the Utah Division of Wildlife Resources (UDWR). Two to six nets, depending on lake or reservoir size, were set at each water in areas less than 30 ft deep. Nets were set during the afternoon and retrieved the following morning. Each net was 1.8 m deep by 38.1 m long and consisted of five monofilament nylon panels with bar mesh sizes of 19.1, 24.4, 31.8, 38.1, and 50.8 mm.

Data recorded for fish gill-netted at each water included numbers, species, and individual lengths. Gill-net samples generally consisted of trout stocked the previous year and a few from stocking 2 years earlier. The trout abundance index used for each reservoir in the study was the mean number of trout collected per net, set overnight (trout per net-night). When comparing trout abundance and estimates of cormorant abundance, we paired the trout abundance index for a given water with the estimate of cormorant abundance for the previous year. Because spring gill-net catches consisted primarily of trout stocked the previous year, the relationship between the cormorant abundance estimate and trout abundance index reflected impacts of predation on one cohort of stocked trout over one year. Large trout were excluded from the data at two waters when calculating the trout abundance index. These larger fish represented older cohorts that were not vulnerable to cormorant predation during the study period. Large trout occurred at Minersville Reservoir and Fish Lake as the result of unusual circumstances or the presence of unique trout populations. At Fish Lake a few large lake trout (*Salvelinus namayacush*) were not used in the index. One cohort of cutthroat trout (*Oncorhynchus clarki*) at Minersville Reservoir was not used in the trout abundance index for that reservoir. This 1986 cohort grew rapidly to a large size following a chemical renovation in 1985 and comprised a substantial portion of the annual spring gill-net catches through 1991. A simple linear regression was used to compare estimates of cormorant abundance (bird-days) and the trout abundance index (trout per net-night) using both untransformed data and log-transformed data.

Data on cormorant diet were collected at three large, lower-elevation reservoirs where birds were relatively abundant. At Minersville and Otter Creek reservoirs, primary potential fish prey species were stocked rainbow trout and Utah chubs, with lesser numbers of cutthroat trout and brown trout (*Salmo trutta*). At Piute Reservoir primary prey species included rainbow trout, Utah chubs, and Utah suckers. Piute Reservoir also contained limited numbers of redside shiners (*Richardsonius balteatus*), smallmouth bass (*Micropterus dolomieui*), cutthroat trout, and brown trout. We collected 10 cormorants each at Minersville, Otter Creek, and Piute reservoirs (30 birds total). Birds were collected using shotguns during July and August at 1000–1100 h following morning feeding periods. We also used food-habit data collected by Wasowicz (1991) at Minersville Reservoir in April 1988, which included cormorants collected during afternoon hours. Additional food-habit information was obtained from six fledgling cormorants at Piute Reservoir in 1989 by approaching active nests and collecting regurgitated stomach contents. In total, diet data were obtained from 52 cormorants, with samples taken in mid-April, late April, late June, late July, early August, and late August.

Stomach contents were identified to fish species using flesh color, peritoneum color, fin rays, and pharyngeal teeth as key characteristics. We made TL measurements of ingested fish when possible. TL estimates were also based on a measurement from the front of the dorsal fin to the front of the anal fin. Estimates of biomass of ingested fish were made using length-weight relationships for each species (Carlander 1969, Varley and Livesay 1976).

Annual trout consumption by cormorants was estimated by multiplying values for bird abundance (bird-days) by a daily biomass consumption rate of 465 g per day (after Wasowicz 1991), and by the percentage of trout in the diet (this study, Wasowicz 1991). The daily biomass consumption rate used by Wasowicz (1991) and this study was based on an average adult body weight for cormorants of 1860 g (Ross 1977) and a daily biomass consumption rate of 25% of body weight. Dunn (1975) reported that daily consumption rates for free-living adults and juveniles of several species of cormorants averaged approximately 20–30% of body weight. When information on diet composition of cormorants was not available for a particular water, we made a conservative estimate of the percentage of trout in the diet by determining relative abundance of trout and other forage species in that water.

Season-long creel surveys of sport fishermen and chemical treatment projects to remove undesirable nongame fish were conducted at a number of study waters. Although not directly related to this study, data collected during these activities provided a means to validate trout abundance indices and verify relative abundance of different fish species. We estimated total annual trout harvest by anglers and the percent return to the creel of the total numbers of fish stocked (Robson 1960, Lambou 1961) during creel surveys. High and low harvest estimates corresponded with high and low trout abundance as measured by standardized gill-netting. Visual inspections following chemical treatments provided another way of verifying relative fish abundance and species composition. Following a chemical treatment, we could be certain that stocked trout dominated a fishery for a year or two. Creel surveys were conducted at Fish Lake in 1989, Johnson Reservoir in 1984 and 1989, Kolob Reservoir in 1991, Lower Bowns Reservoir in 1991, Minersville Reservoir in 1986 and 1988, Newcastle Reservoir in 1991, and Otter Creek Reservoir in 1985. Chemical treatments were conducted at Johnson Reservoir in 1986, Kolob Reservoir in 1985, Koosharem Reservoir in 1985, Minersville Reservoir in 1984 and 1991, Otter Creek Reservoir in 1989, Panguitch Lake in 1991, and Piute Reservoir in 1985 and 1990.

RESULTS

Cormorant Distribution and Abundance

Eight to 35 counts were made at each of the 13 reservoirs (Table 2). Individual counts of cormorants ranged from 0 to 264 birds. Cormorants were observed early in the year (2 February 1989) at Quail Creek Reservoir, which was the lowest in elevation and most southern reservoir studied. At most other waters, cormorants were first observed soon after ice-out, usually in March. Numbers of cormorants were generally highest in spring or early summer. At lower-elevation waters, cormorants were often absent during midsummer but were observed again in late summer or fall. At some higher-elevation waters, highest counts occurred in midsummer. They were present throughout the summer at several of the larger reservoirs. Cormorants were observed at all waters surveyed except one, Lower Bowns Reservoir, the smallest and most easterly located.

Cormorants attempted to nest at 2 of the 13 locations studied. In 1988 and 1989 nesting was initiated at Minersville Reservoir. Cormorants constructed nests in a flooded grove of cottonwood trees in the shallow north end of the reservoir. The nests were abandoned, however, in late spring when the water level receded beyond the nesting trees. Water levels at Minersville Reservoir remained low during the spring of 1990 and 1991. The area in which nesting had been attempted the previous 2 years remained some distance above the shoreline, and cormorants made no further attempts to nest. Cormorants did nest successfully at Piute Reservoir in 1989 and 1990. On 26 June 1989, 45 fledgling cormorants were observed in nests in flooded cottonwood trees in the south end of that reservoir. In 1990, 55 pairs of nesting birds were observed in the same area on 11 April. Young cormorants were observed in 16 of the nests on 26 May 1990, in spite of rapidly dropping water levels that had left nesting trees well above the shoreline. Piute Reservoir was drained in the fall of 1990 causing water levels to remain low in 1991 and exposing the ground below trees used for nesting the previous 2 years. No nesting activity was observed at any of the locations studied in 1991.

Estimates of cormorant abundance at the 13 reservoirs ranged from 0 bird-days at Lower Bowns Reservoir in 1991 to 20,329 bird-days at Otter Creek Reservoir in 1989 (Tables 2 and 3). When we accounted for the size of various waters surveyed, cormorant abundance was highest at Minersville Reservoir where we estimated 34 bird-days per ha for 1989 (Table 4). Cormorant abundance was low at most of the higher-elevation waters, such as Kolob Reservoir, Johnson Reservoir, and Fish Lake.

Trout Abundance

Stocking rates ranged from 186 to 669 trout per ha per year at the waters studied, except at Gunlock Reservoir, which was managed only for warm-water species. In general, numbers and sizes of trout stocked at each reservoir or lake were considered sufficient to produce high numbers of catchable-size trout providing that survival was adequate. Trout abundance indices at the waters surveyed ranged from 1 to 91 trout per net-night (Table 4). Our past experience indicates that trout abundance indices of at least 25–30 fish per net-night yield a population of trout that will produce good fishing during the year. Rainbow trout accounted for the majority of the gill-net catch at most waters. The trout abundance index was inversely related to estimates of cormorant abundance ($P \leq .01$, Fig. 1). Although a log transformation of cormorant abundance data statistically improved the fit of the regression line, the negative relationship was also significant ($P < .05$) for the original, untransformed data. Trout abundance indices were low when bird abundance was greater than 15 cormorant-days per ha. Both high and low trout abundance indices occurred with low cormorant abundance; however, there

TABLE 2. Statistics from cormorant counts at 13 reservoirs in southwestern Utah, 1989–91.

	Time of year			
Water/Year/Statistic	Mar–May	Jun–Aug	Sep–Nov	Total
Otter Creek Reservoir, 1989				
Total days in interval	78	92	52	222
Number of counts	12	7	5	24
Mean birds per count	65	135	56	92
Estimated bird-days	5044	12,394	2891	20,329
Standard error (bird-days)	883	715	947	1479
95% confidence interval	±1765	±1431	±1894	±2958
Otter Creek Reservoir, 1990				
Total days in interval	76	92	61	229
Number of counts	6	6	3	15
Mean birds per count	2	11	8	7
Estimated bird-days	139	1043	488	1670
Standard error (bird-days)	53	563	347	663
95% confidence interval	±107	±1126	±694	±1327
Otter Creek Reservoir, 1991				
Total days in interval	76	92	61	229
Number of counts	5	6	2	13
Mean birds per count	53	7	0	20
Estimated bird-days	4013	675	0	4688
Standard error (bird-days)	1204	357	0	1256
95% confidence interval	±2407	±714	±0	±2511
Newcastle Reservoir, 1989				
Total days in interval	92	92	91	275
Number of counts	9	6	7	22
Mean birds per count	6	0	1	2
Estimated bird-days	593	0	65	658
Standard error (bird-days)	114	0	52	125
95% confidence interval	±228	±0	±103	±250
Newcastle Reservoir, 1991				
Total days in interval	92	92	31	215
Number of counts	18	18	3	39
Mean birds per count	3	t[a]	1	1
Estimated bird-days	240	15	21	276
Standard error (bird-days)	103	8	21	105
95% confidence interval	±206	±17	±41	±210
Minersville Reservoir, 1989				
Total days in interval	92	92	56	240
Number of counts	14	12	7	33
Mean birds per count	78	33	11	45
Estimated bird-days	7209	3067	624	10,900
Standard error (bird-days)	1785	475	190	1856
95% confidence interval	±3569	±949	±379	±3712
Minersville Reservoir, 1990				
Total days in interval	92	92	61	245
Number of counts	12	11	2	25
Mean birds per count	64	14	3	30
Estimated bird-days	5850	1296	153	7299
Standard error (bird-days)	1265	317	153	1313
95% confidence interval	±2529	±634	±305	±2625
Minersville Reservoir, 1991				
Total days in interval	92	92	30	214
Number of counts	7	6	2	15
Mean birds per count	31	1	0	14
Estimated bird-days	2852	107	0	2959
Standard error (bird-days)	963	77	0	966
95% confidence interval	±1926	±153	±0	±1931

TABLE 2. Continued.

	Time of year			
Water/Year/Statistic	Mar–May	Jun–Aug	Sep–Nov	Total
Piute Reservoir, 1989				
Total days in interval	82	92	91	265
Number of counts	11	7	8	26
Mean birds per count	70	65	12	48
Estimated bird-days	5702	5967	1081	12,750
Standard error (bird-days)	690	1358	605	1639
95% confidence interval	±1380	±2715	±1209	±3277
Piute Reservoir, 1990				
Total days in interval	92	92	0	184
Number of counts	7	6	0	13
Mean birds per count	60	29	0	45
Estimated bird-days	5559	2683	0	8242
Standard error (bird-days)	1395	670	0	1548
95% confidence interval	±2790	±1341	±0	±3095
Piute Reservoir, 1991				
Total days in interval	82	92	—	174
Number of counts	5	6	—	11
Mean birds per count	2	5	—	4
Estimated bird-days	180	475	—	655
Standard error (bird-days)	160	196	—	253
95% confidence interval	±320	±392	—	±506
Fish Lake, 1989				
Total days in interval	82	92	74	248
Number of counts	4	6	5	15
Mean birds per count	0	t	0	t
Estimated bird-days	0	15	0	15
Standard error (bird-days)	0	15	0	15
95% confidence interval	±0	±31	±0	±31
Panguitch Reservoir, 1989				
Total days in interval	71	92	73	236
Number of counts	4	5	5	14
Mean birds per count	1	6	5	4
Estimated bird-days	71	570	365	1006
Standard error (bird-days)	71	128	247	287
95% confidence interval	±142	±256	±493	±573
Panguitch Reservoir, 1990				
Total days in interval	49	92	61	202
Number of counts	7	12	3	22
Mean birds per count	6	25	13	17
Estimated bird-days	301	2285	773	3359
Standard error (bird-days)	121	175	458	505
95% confidence interval	±242	±349	±917	±1010
Panguitch Reservoir, 1991				
Total days in interval	30	92	0	122
Number of counts	2	6	0	8
Mean birds per count	0	5	0	4
Estimated bird-days	0	429	0	429
Standard error (bird-days)	0	272	0	272
95% confidence interval	±0	±543	±0	±543

TABLE 2. Continued.

	Time of year			
Water/Year/Statistic	Mar–May	Jun–Aug	Sep–Nov	Total
Koosharem Reservoir, 1989				
Total days in interval	92	92	11	195
Number of counts	10	6	2	18
Mean birds per count	0	1	1	t
Estimated bird-days	0	46	6	52
Standard error (bird-days)	0	21	6	21
95% confidence interval	±0	±41	±11	±43
Johnson Reservoir, 1989				
Total days in interval	31	92	58	181
Number of counts	3	6	4	13
Mean birds per count	0	t	0	t
Estimated bird-days	0	31	0	31
Standard error (bird-days)	0	31	0	31
95% confidence interval	±0	±61	±0	±61
Enterprise Reservoir, 1989				
Total days in interval	71	92	88	251
Number of counts	9	6	6	21
Mean birds per count	4	1	t	1
Estimated bird-days	252	77	29	358
Standard error (bird-days)	147	50	29	158
95% confidence interval	±295	±100	±59	±317
Lower Bowns, 1991				
Total days in interval	31	92	61	184
Number of counts	6	17	12	35
Mean birds per count	0	0	0	0
Estimated bird-days	0	0	0	0
Standard error (bird-days)	0	0	0	0
95% confidence interval	±0	±0	±0	±0
Kolob Reservoir, 1991				
Total days in interval	31	92	61	184
Number of counts	3	18	14	35
Mean birds per count	t	t	t	t
Estimated bird-days	10	5	4	19
Standard error (bird-days)	10	5	4	12
95% confidence interval	±21	±10	±9	±25
Gunlock Reservoir, 1989				
Total days in interval	92	92	91	275
Number of counts	10	7	6	23
Mean birds per count	8	0	t	3
Estimated bird-days	727	0	15	742
Standard error (bird-days)	296	—	15	297
95% confidence interval	±592	±0	±30	±593
Quail Creek Reservoir, 1989				
Total days in interval	92	92	91	275
Number of counts	12	7	6	25
Mean birds per count	3	0	1	1
Estimated bird-days	284	0	91	375
Standard error (bird-days)	167	—	30	170
95% confidence interval	±334	—	±60	±339

[a]t = cormorants present but mean number of birds per count was less than 0.1.

TABLE 3. Estimated annual consumption of fish by cormorants at 13 reservoirs in southwestern Utah, 1989–91.

Water	Year	Survey period	Total bird-days (95% C.I.)	Estimated[a] annual fish consumption (kg)	Percent trout in diet	Annual trout consumption (kg)
Lower Bowns	91	1 May–31 Oct	0 (±0)	0	—	0
Enterprise	89	22 Mar–27 Nov	358 (±317)	166	100^{c}	166
Fish Lake	89	10 Apr–13 Nov	15 (±31)	7	80^{c}	6
Gunlock	89	1 Mar–30 Nov	742 (±593)	345	0	0
Johnson	89	1 May–28 Oct	31 (±61)	14	80^{c}	12
Kolob	91	1 May–28 Oct	19 (±25)	9	100^{c}	9
Koosharem	91	1 Mar–11 Sep	52 (±43)	24	80^{c}	19
Minersville	89	1 Mar–26 Oct	10,900 (±3712)	5069	44^{b}	2230
Minersville	90	1 Mar–31 Oct	7299 (±2625)	3394	44^{b}	1493
Minersville	91	1 Mar–30 Oct	2959 (±1931)	1376	44^{b}	605
Newcastle	89	1 Mar–30 Nov	658 (±250)	306	80^{c}	245
Newcastle	91	1 Mar–10 Oct	276 (±210)	128	80^{c}	103
Otter Creek	89	14 Mar–21 Oct	20,329 (±2958)	9453	80^{b}	7562
Otter Creek	90	16 Mar–31 Oct	1670 (±1327)	777	90^{c}	699
Otter Creek	91	16 Mar–31 Oct	4688 (±2511)	2180	90^{c}	1962
Panguitch	89	21 Mar–12 Nov	1006 (±573)	468	80^{c}	374
Panguitch	90	12 Apr–31 Oct	3359 (±1010)	1562	80^{c}	1250
Panguitch	91	2 May–31 Aug	429 (±543)	199	80^{c}	160
Piute	89	10 Mar–30 Nov	12,750 (±3277)	5929	55^{b}	3261
Piute	90	1 Mar–31 Aug	8242 (±3095)	3833	55^{b}	2108
Piute	91	10 Mar–31 Aug	655 (±506)	305	80^{c}	244
Quail Creek	89	1 Mar–30 Nov	375 (±339)	174	44^{c}	77

[a] Estimated annual consumption was calculated using a daily consumption rate of 465 g per bird per day and assuming only fish were eaten.
[b] Based on food habit data collected at given waters during this study (Table 5).
[c] Based on conservative estimates from relative abundance of forage species in gill-netting samples and history of the reservoir.

were no cases that had both a high trout abundance index and high bird abundance.

Cormorant Food Habits

Stomach contents from 30 adult and 6 nestling cormorants from three reservoirs were examined (Table 5). Stomachs from 7 (23%) of the 30 adults were empty. Food items identified were primarily trout and Utah chubs. One smallmouth bass and one crayfish were identified from collections taken at Piute Reservoir. Trout accounted for 24–81% (biomass) of the diet of cormorants at the three locations sampled. During similar sampling in April 1988, Wasowicz (1991) reported that trout comprised 97% of the diet of cormorants at Minersville Reservoir. Trout in the stomach samples from the three locations ranged in size from 100 to 396 mm TL, although most trout had been stocked about 10 months earlier and were typically greater than 230 mm TL. Utah chubs comprised 19–76% of the cormorant diet by weight. Utah chubs from stomach samples were 48–275 mm TL. Most cormorants contained only one species of prey. Only two of the birds examined contained both Utah chubs and trout.

Estimates of the annual total biomass of fish consumed by cormorants ranged from 0 kg at Lower Bowns Reservoir to 9453 kg at Otter Creek Reservoir (Table 3). Based on reservoir area, Minersville Reservoir had the highest estimated annual consumption of fish at 15.8 kg per ha. Estimates of annual trout biomass consumed by cormorants ranged from 0 to 7562 kg.

DISCUSSION

Distribution, relative abundance, and seasonal occurrence of cormorants in Utah has changed over the past decade. After a review of the available information and following visits to all recorded nesting sites in the state, Mitchell (1977) concluded that the population of cormorants in Utah had been steadily decreasing for the past 50 years. He reported that the total known cormorant population of Utah in 1973 consisted of only 386 cormorants nesting in five colonies, all associated with the Great Salt Lake or Utah Lake. More recently, Walters and Sorenson (1983) listed the cormorant only as a spring and/or fall migrant south of latitude 39°N in Utah. Hedges (1986)

TABLE 4. Estimates of cormorant abundance compared to trout abundance indices at southwestern Utah reservoirs, 1989–92.

	Sample Years							
Water	Cormorant abundance estimate	Trout density index	Letter identification	Estimated total bird-days (95% C.I.)	Mean reservoir surface area (ha)	Bird-days per ha (95% C.I.)	Number of gill-nets	Trout per net-night[a]
Lower Bowns	1991	1992	A	0 (±0)	27	0 (±0)	2	26
Enterprise	1989	1990	B	358 (±317)	150	2.4 (±2.1)	2	69
Fish Lake	1989	1990	C	15 (±31)	1000	t[c] (±0)	6	15[b]
Johnson	1989	1990	D	31 (±61)	214	0.1 (±0.3)	3	91
Minersville	1989	1990	E	10,900 (±3712)	321	34.0 (±11.5)	4	3[b]
Minersville	1990	1991	F	7299 (±2625)	301	24.2 (±8.7)	4	1[b]
Newcastle	1989	1990	G	658 (±250)	53	12.4 (±4.7)	3	6
Newcastle	1991	1992	H	276 (±210)	50	5.5 (±4.2)	4	27
Otter Creek	1990	1991	I	1670 (±1327)	765	2.2 (±1.7)	3	39
Otter Creek	1991	1992	J	4688 (±2511)	765	6.1 (±3.3)	4	13
Panguitch	1989	1990	K	1006 (±573)	450	2.2 (±1.2)	3	15
Panguitch	1990	1991	L	3359 (±1010)	400	8.4 (±2.5)	3	31
Piute	1989	1990	M	12,750 (±3277)	812	15.7 (±4.0)	4	18

[a] Trout abundance index was calculated as the mean number of trout collected per net-night during standardized spring gill-net sampling.

[b] Trout abundance indices did not include large trout collected at two reservoirs as explained in text.

[c] t = less than 0.1 bird-days per ha.

also reported that cormorants were only spring and fall migrants at Minersville Reservoir from 1983 through 1986. During our study cormorants were summer residents at Minersville Reservoir in 1989 and 1990. They were also present through the summer in 1989, 1990, and 1991 at Piute and Otter Creek reservoirs. At Panguitch Lake, cormorants were summer residents during 1989 and 1990. As noted above, cormorants nested successfully in at least one location in southwestern Utah in 1989 and 1990. The single highest count of cormorants at Minersville during 1988 (Wasowicz 1991) was nearly as high as the total Utah population of cormorants in 1973 (Mitchell 1977).

Changes in cormorant abundance and distribution observed in southwestern Utah coincide with reported increases of cormorants in other areas of Utah and in the rest of North America. New rookeries have been reported at Hyrum Reservoir, Cache County, Utah (T. Pettengill, UDWR, personal communication), and Mona Reservoir, Juab County, Utah (D. Shirley, UDWR, personal communication). Large increases in the number of cormorants in other regions of North America since the early 1900s have been well documented (Price and Weseloh 1986, Christie et al. 1987, Campo et al. 1988, Findholt 1988). Factors cited for the increases nationwide include protection of cormorants by federal and state statutes, prohibitions against the use of chlorinated hydrocarbons as pesticides, and the creation of new suitable habitats. Changes in cormorant distribution and abundance in Utah are a function of the same factors as well as others peculiar to the state. Increases reported at various locations in Utah occurred after a rise in the water level of the Great Salt Lake in the mid-1980s. There was considerable loss of habitat and food supplies for cormorants in northern Utah as freshwater marshes surrounding the lake were inundated by saltwater. At the same time, annual precipitation in southern Utah was also above normal, which resulted in increases in the amount of cormorant habitat in that area. Consequently, some of the increase in cormorant numbers observed in parts of Utah may have been caused by displacement of birds from the Great Salt Lake marshes. As conditions changed again in the early 1990s, cormorants returned to former habitats in northern Utah. Numbers of birds at locations in southwestern Utah have decreased in general since 1989. Drought conditions in recent years throughout the state have resulted in decreased habitat in southwestern Utah, as evidenced by the loss of nesting areas at Minersville and Piute reservoirs. At the same time, habitat conditions for cormorants in northern Utah have improved to some extent, as the Great Salt Lake receded and freshwater marsh habitat again became more available.

It is possible that collections of cormorants at the three waters where food habits were

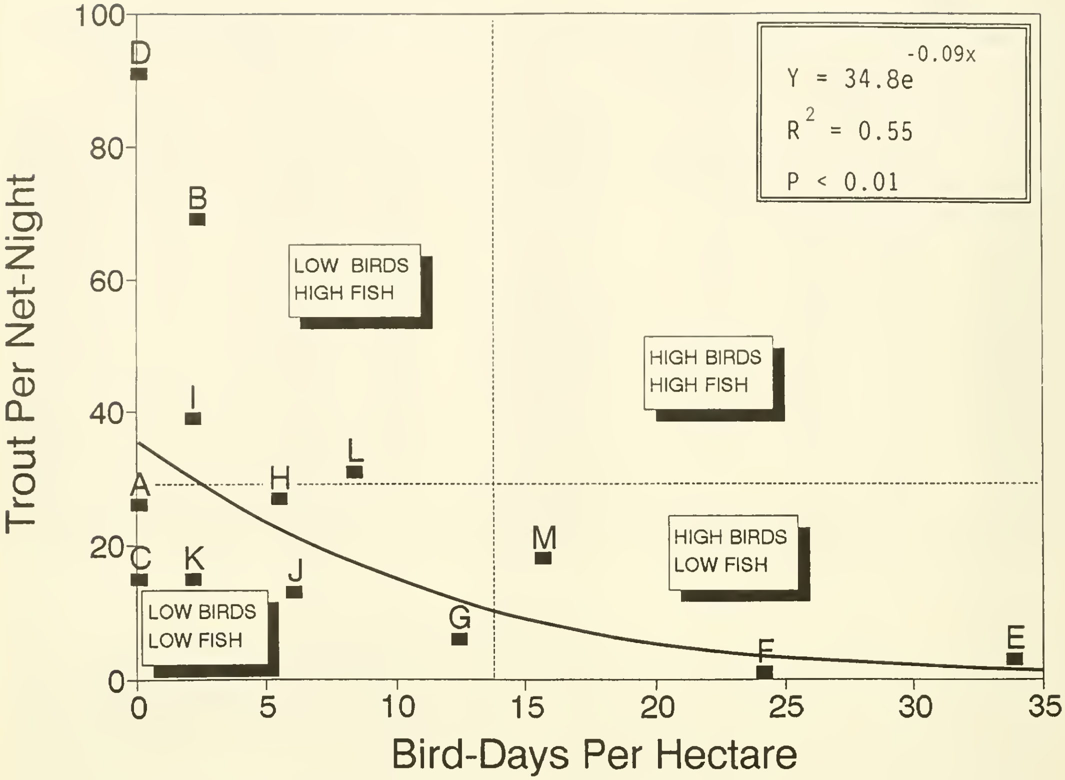

Fig. 1. Regression plot showing relationship between the catch of trout in gill-nets and estimates of cormorant abundance at 13 reservoirs in southwestern Utah, 1989–91. Individual data points are labeled to correspond to location and year as listed in Table 4.

studied could have had some impact on numbers of birds and estimates of abundance following their removal. We collected cormorants only at waters where they were most abundant, however, and felt any impact was minimal. At Minersville Reservoir, for example, the 10 cormorants collected represented a loss of approximately 710 bird-days, or 6.5% of a total of 10,900 bird-days for the year.

Confidence limits for estimates of cormorant abundance (bird-days) averaged 43% of the estimate for reservoirs with high numbers of cormorants (greater than 1000 bird-days). For reservoirs where cormorants were less abundant, confidence intervals were wider, but within reason when absolute values are considered. In many ways the survey of cormorants was more precise than a typical creel survey of fishermen. Count data were less variable and were obtained more directly than in most creel surveys. Numbers of cormorants, for example, were less subject to sudden changes due to weather and did not change because of weekends and holidays. Cormorant fishing abilities and consumption rates were also more consistent and not as variable as catch rates among anglers. Confidence intervals were not included for our estimates of the amount of fish consumed by cormorants. Statistics for cormorant abundance (bird-days) provide some indication of the level of confidence that may be expected for estimates of fish consumption by cormorants (Table 3).

Estimates of annual consumption of fish by cormorants in this study were based on a daily consumption rate of 25% of body weight and an average adult body weight of 1860 g (Ross 1977). However, counts of cormorants at the study waters also included nestlings in some instances. Values calculated for fish consumption where nestlings were present would tend to overestimate actual consumption because of their smaller size and lower caloric intake. Nestlings were present at only one study water, however, and after 25 days of age, their consumption rates are similar to those of adults

TABLE 5. Fish in the diet of Double-crested Cormorants at three reservoirs in southwestern Utah, 1988 and 1989. Data from analysis of stomach contents (SC) from sacrificed adults and regurgitations (R) from nestlings.

			Trout		Utah chub		Smallmouth bass	
Location/date	Sampling method	Sample size / # empty	% of total biomass	Size range (TL, mm)	% of total biomass	Size range (TL, mm)	% of total biomass	Size range (TL, mm)
Minersville Res. 17, 24 April 1988 (from Wasowicz 1991)	SC	16/6	97	65–262	3	—	—	—
Minersville Res. 27 Jul, 29 Aug 1989	SC	10/3	44	100–396	56	76–138	—	—
Otter Creek Res. 4, 24 Aug 1989	SC	10/2	81	322–339	19	48–128	—	—
Piute Res. 4, 24 Aug 1989	SC	10/2	74	145–396	24	62–153	2	110
Piute Res. 29 June 1989	R	6	24	178–300	76	89–275	—	—

(Dunn 1975). Consequently, any overestimate bias was considered to be negligible. Estimates of fish consumption should be considered rough estimates or potential consumption. Nevertheless, it was obvious that cormorants consumed a significant number of fish, including trout, at some reservoirs.

There is a wide range of observation in the literature concerning the impact of cormorants on associated fisheries. Cormorants feed almost exclusively on fish. They are opportunistic feeders and often consume the most available prey item (Trautman 1951, Belonger 1983, Pilon et al. 1983, Craven and Lev 1987). In many instances forage fish have comprised the majority of the diet (Baillie 1947, Craven and Lev 1987, Campo et al. 1988, Carroll 1988), and their impact on sportfisheries was considered negligible. Campo et al. (1988) reported that size and species of fish consumed were highly variable by location and time. They found that cormorants generally consumed forage species unless recreational fish were the predominant species available. In some instances, however, cormorants had a substantial impact on recreational fisheries. Significant predation by cormorants on stocked Atlantic salmon smolts in Maine has been documented for almost 50 years (Cormorant Study Committee 1982). Belonger (1983) estimated that cormorants consumed a total of 1,869,033 yellow perch at lower Green Bay, Lake Michigan, from June through September 1982. In Utah, Wasowicz (1991) estimated that cormorants consumed 9,900 (13%) of 74,000 fingerling rainbow trout during a 2-week period following their stocking at Minersville Reservoir. In addition to the loss of stocked fingerling trout, cormorants ate four times the biomass of larger trout compared to fingerlings. The estimated consumption of catchable-size trout by loons and cormorants at Minersville in 1988 was greater than the estimated sportfish harvest by anglers. Our study suggests that cormorants had a negative impact on some put-grow-and-take trout fisheries throughout southwestern Utah. Potential consumption of trout by cormorants was generally estimated to be higher at the larger, lower-elevation reservoirs. The impact of cormorant predation on sportfish was greatest at Minersville and Otter Creek reservoirs. Potential consumption of trout at those two waters was estimated to be greater than 5 kg per ha for at least one year during the study. Potential consumption of trout by cormorants was moderate (3–4 kg per ha) at Piute Reservoir, Newcastle Reservoir, and Panguitch Lake. The impact of cormorants on sportfisheries at the remaining waters was relatively low.

Although the inverse relationship between cormorant abundance and trout abundance is open to interpretation, it does suggest that predation by piscivorous birds plays an important role in sportfisheries management. A number of factors tend to mask an even stronger relationship between cormorants and trout. For example, survival of stocked trout has been shown to be related to size at stocking, with larger fish generally showing better survival and return to anglers (Burdick and Cooper 1956, Pycha and King 1967, Hansen and Stauffer 1971). Consequently, fishery managers have responded to low survival in southwestern Utah reservoirs by increasing the size and/or number of stocked fish, as well as adjusting stocking times. Reservoirs with histories of low trout survival due to various causes, including bird predation, generally were stocked with larger fish at times when cormorants were not abundant, compared with reservoirs where trout survival was higher. Despite these differential management efforts, an inverse relationship between cormorants and fish abundance has persisted.

Certainly, there are many other biotic as well as abiotic factors that influenced trout abundance in the study waters, as illustrated by instances where both trout abundance and bird abundance were low. At the 13 waters observed during this study, however, there were no instances of a high trout abundance index (greater than 30 fish per net-night) associated with high cormorant abundance (greater than 14 bird-days per ha). Conversely, in all cases where trout abundance was high, cormorant abundance was low. This study was designed to document the abundance of cormorants at waters in southwestern Utah and examine the relationship between cormorant numbers and trout abundance. During the course of the study, it became obvious that many factors, including elevation, reservoir size, and geographic location, influenced numbers of cormorants at a particular water as well as relative abundance of trout. Although determining which environmental factors influenced cormorant numbers at a given water would be of interest, it was beyond the scope of this study.

Cormorants apparently selected trout over other species of fish at the three reservoirs where food habits were studied. All three reservoirs contained relatively dense populations of Utah suckers and/or Utah chubs in addition to trout. Trout, however, may have represented the largest easily available prey item. Knopf and Kennedy (1981) observed that cormorants pursue larger fish in a school.

Certain fisheries are particularly vulnerable to predation by cormorants. The cormorant is able to consume large prey fish (Campo et al. 1988, this study), is able to key on available food sources quickly (Barlow and Bock 1984), and will travel up to 45 km daily to feed (Moerbeek et al. 1987). These characteristics have made aquaculture stations and commercial harvesting operations especially susceptible to predation by cormorants (Schramm et al. 1984, Omand 1947). Many of the recreational trout fisheries in Utah have similarities to aquaculture operations and, consequently, are also vulnerable to predation by cormorants. Utah's sportfisheries typically are managed on a put-grow-and-take basis, where small hatchery-reared rainbow trout are stocked annually. Trout are generally stocked in the spring with the intent that anglers will harvest them after they grow to a catchable size. Stocking often occurs prior to or during the spring migration season for cormorants. Many of the stocked waters also contain few alternate prey species. This scenario often results in a relatively dense population of vulnerable sportfish in waters at the time when cormorant numbers are highest.

Although predation by cormorants and other piscivorous species of birds in Utah represents a serious challenge in sportfisheries management, these birds are also an important component of aquatic ecosystems throughout the West. Their intrinsic value has been recognized by both wildlife managers and the general public, and they have been protected strictly by both state and federal statutes. Dombeck et al. (1984) recognized the importance of incorporating the needs of piscivorous birds into fisheries management objectives. In the past, consideration of avian piscivores has often been restricted to attempts at limiting their potential impact on sportfish or commercial harvest. Methods employed to limit losses of sportfish or commercially valuable fish to bird predation have included gunning, nest and egg destruction, hazing, removal of roost trees, covering aquaculture facilities, and creation of alternative feeding sites. Efforts to control the numbers of cormorants are now regulated strictly under the Migratory Bird Treaty and state statutes. Direct control by gunning is still permitted in some areas under certain circumstances but has been largely ineffective and has generated adverse public opinion where practiced (L. N. Flagg, Maine Department of Marine Resources, personal correspondence). Hazing and construction of physical barriers are impractical at waters other than small ponds. There are a number of measures, however, that can mitigate the impact of cormorant predation on sportfisheries as well as enhance the available habitat for cormorants. In regions where cormorants are primarily migrants, fish stocking should be timed to avoid periods of peak bird abundance. Certain species of sportfish are less vulnerable to bird predation (Matkowski 1989) and might be used in situations where predation is a factor. Given the adaptable nature of cormorants and their mobility, it may also be possible to create alternate habitats where conflicts will not arise. In virtually every region of Utah there are waters with low suitability for sportfish management that might lend themselves to management as "forage" waters for piscivorous birds. Maintaining populations of suitable forage species and providing other elements attractive to cormorants, such as roosting sites and seclusion at selected waters, may at least partially relieve predation pressure on more important sportfisheries. It may be necessary in some instances simply to adjust stocking rates to accommodate some degree of bird predation. At Minersville Reservoir the UDWR has initiated a new sportfish management program integrating piscivorous birds into the overall reservoir management. Proposed changes at Minersville include altering the timing of stocking as well as increasing the size of fish stocked, addition of new species of sportfish, and angling regulations designed to maintain a population of larger trout less vulnerable to predation.

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NEW MAMMAL RECORD FOR FREMONT ISLAND WITH AN UPDATED CHECKLIST OF MAMMALS ON ISLANDS IN THE GREAT SALT LAKE

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Key words: Great Salt Lake, Reithrodontomys megalotis, Peromyscus maniculatus, *mammals, island biogeography, Fremont Island.*

Islands of the Great Salt Lake were first visited by Europeans when a party led by Fremont (1850) landed on Fremont Island in the northeast arm of the lake. Fremont named the island "Disappointment Island" due to its lack of fresh water and timber, although the island is somewhat of a disappointment to a mammalogist as well, with only three species of mammals recorded. Deer mice (*Peromyscus maniculatus*), jackrabbit (*Lepus californicus*), and ground squirrel (probably *Spermophilus townsendii*) have been found on the third largest island (approximately 1300 ha) in the lake (Goldman 1939, Marshall 1940). Goldman (1939) ascribed subspecific status (*P. m. inclarus*) to deer mice from Fremont Island based on pelage differences from the mainland *P. m. sonoriensis*. One specimen of jackrabbit was taken by Marshall (1940), who reported that, in addition to being recent immigrants, they were also scarce. According to sheepherders on the island, rabbits may have crossed in the winter over ice and debris from Bear River during winter of 1933–34. The ground squirrel was a single specimen observed by Stansbury (Marshall 1940), who considered it an anomaly.

Surveys of the islands in 1937 and 1938 (Goldman 1939, Marshall 1940) were performed during a historic low in lake levels, when many islands were actually peninsulas connected to the mainland by sandbars. However, Fremont is one of the few Great Salt Lake islands that has been nearly continuously isolated from the mainland during the historic record and probably into the evolutionary past (Arnow and Stephens 1990). Marshall (1940) reported that the island had been connected with the mainland by a sandbar 20 miles to the eastern shore of the lake for 3 years since 1850 (the beginning of lake-level records) when lake levels were near 4194 feet. Since 1938, lake levels were continuously below 4195 feet from 1959 to 1971, possibly providing periodic connections over mudflats with the mainland at that time (Arnow and Stephens 1990).

Since the 1938 census, publications concerning the Great Salt Lake islands' fauna have been limited to literature reviews (Rawley et al. 1974, Gwynn 1980), with no new sampling efforts reported until recently. However, even brief studies on islands other than Fremont have revealed substantial changes in their species lists since those compiled by Bowers (1982), who relied primarily on the 1938 census. Marti (1986), in a study of Barn Owl diets on Antelope Island, recorded six new mammal species for that island, including a shrew, two voles, and two rather common Great Basin species, the Great Basin pocket mouse (*Perognathus parvus*) and the western harvest mouse (*Reithrodontomys megalotis*). Paul (1983) reported that badger and fox occur on Antelope island. Cramer et al. (1990) also reported dramatic changes in species composition of mammals on Dolphin Island. Given the recent additions of common species to some islands' species lists (Table 1), the relatively low trapping effort of the 1938 census (e.g., only 37 trap nights on Dolphin Island), and the unusually impoverished fauna recorded for Fremont Island, I spent 3 days and 2 nights (20–23 June 1992) trapping on Fremont Island to determine whether known mammal records

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TABLE 1. Current records of species by island for mammals in the Great Salt Lake. Key: 1–Goldman (1939), Marshall (1940), Durrant (1952); 2–Cramer et al. (1990); 3–Marti (1986); 4–Paul (1983); 5–present study.

	Island						
Species	Bird	Dolphin	Gunnison	Carrington	Fremont	Stansbury	Antelope
Sorex sp.							3
Dipodomys microps		1	1	1		1	
Dipodomys ordii	1	2		1		1	1
Perognathus parvus				1		1	3
Perognathus longimembris		2					
Thomomys bottae						1	1
Eutamias minimus						1	
Spermophilus townsendii					1	1	1
Erethizon dorsatum		1				1	
Peromyscus crinitus						1	
Peromyscus maniculatus	1	1	1	1	1	1	1
Reithrodontomys megalotis					5	1	3
Neotoma lepida		1		1		1	1
Onychomys leucogaster						1	
Ondatra zibethicus							3
Microtus montanus							3
Microtus pennsylvanicus							3
Sylvilagus nuttalli				1		1	1
Lepus californicus					1	1	1
Odocoileus hemionus						1	1
Antilocapra americana							1
Lynx rufus						1	1
Mustela frenata							1
Taxidea taxus						1	4
Mephitis mephitis						1	1
Vulpes vulpes							4
Canis latrans	1	1		1		1	1
Maximum species recorded	3	7	2	7	4	19	21
Most recent # species	3	2	2	7	2	19	21
Total island area (ha)	9	21	67	730	1217	7977	10,767

could be scarce due to inadequate sampling effort. In a short sampling period, I anticipated the possibility of catching common Great Basin species such as heteromyids (whose unusual absence was commented on by Marshall [1940]) and verifying anecdotal reports of ground squirrels and jackrabbits on the island.

On the first night of trapping, I set out 160 Sherman live-traps in three localities on the island. Ninety traps were set near Beacon Hill by the north shore of the island. Thirty were set near the north shore north of Castle Rock, and the remaining 40 were set in more diverse habitat at higher elevations (1450–1500 m) just below Castle Rock on its north-facing slope. Twenty-four deer mice (*Peromyscus maniculatus*) were captured on these three areas. Those traps were left in place for a second night, and an additional 60 traps were set near the southeast point of the island in an area with very sandy soils. The following morning 40 deer mice and one western harvest mouse (*Reithrodontomys megalotis*) were collected. Total trapping success was 17%, but was twice as high (30%) at the high-altitude location near Castle Rock compared to other locations (G-test, G = 9.71, $P < .005$). I suspect the high capture rate was due to the habitat, which had more shrub cover (much of the island is monospecific stands of cheatgrass, *Bromus tectorum*) and broken, rocky terrain that could provide ample shelter and nest sites.

Thirty-six percent of the deer mice captured were juveniles, and the sex ratio was slightly biased toward males (56%). The single harvest mouse collected was an adult scrotal male and the first harvest mouse recorded on the island. The specimen was deposited as a skin and skeleton in the Utah Museum of Natural History at the University of Utah (catalog #29260).

No other small mammals were captured, nor was any evidence of their presence on the island recorded. I surveyed the island for evidence of mammals previously recorded there, including black-tailed jackrabbits and Townsend ground squirrels. Jackrabbits reported on the island in 1938 clearly did not persist. The complete absence of rabbit fecal pellets was particularly convincing evidence of the absence of rabbits on this island, although the remains of one were found near a Golden Eagle (*Aquila chrysaetos*) nest. The lone ground squirrel recorded by Stansbury was obviously not part of a viable island population. I saw no ground squirrels nor any evidence of burrows or runways. Other small mammals common to the area such as desert woodrats (*Neotoma lepida*), pocket mice (*Perognathus* sp.), and kangaroo rats (*Dipodomys* sp.) are also conspicuously absent from Fremont Island. I saw no evidence of heteromyid burrows, particularly in apparently suitable habitat on the southeast corner of the island. Rocky crevices, normally common nest sites for desert woodrats, were completely unused; I found no nests or fecal material.

Clearly, Fremont Island is truly depauperate in mammalian fauna. Apparently, deer mice and western harvest mice are the only native mammals on the island, and many species common to the adjacent mainland are absent. The island is much larger than Carrington Island, which supports six species of mammals. Similarly, Gunnison, Bird, and Dolphin islands all support two species of mammals on much smaller areas. It is tempting to suggest that the more isolated nature of Fremont Island and probable lack of frequent immigration have led to its simple mammalian fauna. Habitat area and diversity may also be factors affecting successful colonization since much of the island's original bunchgrass and shrub cover has been reduced by fire, grazing, and cheatgrass invasion.

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MYCORRHIZAL COLONIZATION, HYPHAL LENGTHS, AND SOIL MOISTURE ASSOCIATED WITH TWO *ARTEMISIA TRIDENTATA* SUBSPECIES

James D. Trent[1], Tony J. Svejcar[2], and Robert R. Blank[1]

ABSTRACT.—Mycorrhizal fungi are thought to benefit associated plant species via enhanced nutrient uptake and/or improved water relations. However, detailed descriptions of the components of mycorrhizal colonization and mycorrhizal hyphal growth are not available for *Artemisia tridentata*. This species occupies sites characterized by relatively low levels of both soil nutrients and moisture. We studied patterns of vesicular, arbuscular, and hyphal mycorrhizal colonization, mycorrhizal hyphal lengths, and soil moisture associated with two subspecies of *A. tridentata* over a 2-year period. *A. tridentata* ssp. *vaseyana* (ATV) is generally associated with more mesic and slightly higher elevation sites compared to *A. tridentata* ssp. *tridentata* (ATT). Nearly twice as much precipitation was received the first year compared to the second. In general, there were higher levels of colonization and hyphal lengths associated with ATV than with ATT. The ATV site received slightly more precipitation and was lower in available nutrients than the ATT site. Hyphal lengths and arbuscular colonization appeared more responsive to precipitation than were either vesicular or hyphal colonization. Hyphal colonization did not necessarily follow the same temporal pattern as hyphal lengths. Thus, mycorrhizal activity was greater for the subspecies that received slightly more precipitation and occupied a site lower in available nutrients. Arbuscular colonization and hyphal lengths appeared to be most closely associated with soil moisture and thus plant activity.

Key words: vesicular-arbuscular mycorrhizae, hyphal length, Artemisia tridentata, *soil moisture, soil temperature.*

Understanding ecosystem processes requires baseline data that describe spatial and temporal variations in microbial mediated processes (Burke et al. 1989). Such information is also needed to assess the role of mycorrhizae and other fungi in native plant communities. In native plant communities, vesicular-arbuscular mycorrhizal (VAM) colonization has been shown to vary both seasonally and among plant species (Read et al. 1976, Rabatin 1979, Daft et al. 1980, Gay et al. 1982, Allen 1983, Giovannetti 1985, Brundrett and Kendrick 1988). Morphogenesis of arbuscule and vesicle formation should be differentiated when assessing functionality or dependency of the plant on VAM on a seasonal basis. The presence of arbuscules indicates plant-fungal interactions (Hirrel et al. 1978, Allen 1983) since arbuscules are the site for P and C transfer between symbionts (Cox and Tinker 1976, Wilcox 1993). Seasonal changes in extramatrical VAM fungal hyphae indicate that plant-fungal interactions are dynamic (Wilcox 1993). Therefore, it is necessary to measure seasonality of arbuscular colonization and extramatrical hyphae to adequately assess the changing relationship between symbionts in the field.

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The Great Basin environment is characterized by winter precipitation, normally as snow, followed by hot, dry summers (Comstock and Ehleringer 1992). Root growth is most abundant in upper soil horizons in the early spring. Rooting activity diminishes in upper soil horizons as root growth follows the soil moisture profile into deeper soil layers (Fernandez and Caldwell 1975). In desert soils, N and P are most abundant in upper soil horizons (West 1991), and their availability to plants diminishes with decreasing soil moisture. Moisture movement from deep roots in moist soils to shallow roots in dry soils could make shallow soil nutrients available through the process of hydraulic lift (Passioura 1988, Caldwell and Richards 1989, Caldwell et al. 1991). Mycorrhizae could play a role in this process (Richards and Caldwell 1987, Caldwell et al. 1991); however, little is known about seasonal dynamics of mycorrhizae in arid ecosystems.

Fitter (1993) suggests that plant root systems evolve in a manner that optimizes the use of plant carbon. Mycorrhizal colonization and the formation of extramatrical hyphae should also reflect an optimization of plant carbon usage. But to date there is relatively little information on spatial or temporal variation in mycorrhizal activity in the Great Basin. In this study we quantified VAM arbuscular root colonization, vesicular root colonization, hyphal root colonization, and mycorrhizal hyphal length through the plant growing season for 2 years in *Artemisia tridentata* ssp. *tridentata* and *Artemisia tridentata* ssp. *vaseyana*. We have characterized the seasonality of the above parameters and show their relationship to changes in both soil moisture and temperature.

STUDY SITE DESCRIPTION

An *Artemisia tridentata* ssp. *tridentata* (ATT) and an *Artemisia tridentata* ssp. *vaseyana* (ATV) plant community were chosen for study. The study sites are located approximately 30 miles northwest of Reno, Nevada, and are within 3 miles of each other. The ATT community is at 1555 m elevation and is composed of the following vegetation: *Artemisia tridentata* ssp. *tridentata*, *Chrysothamnus viscidiflorus*, *Ephedra viridis*, *Stipa comata*, *S. thurberiana*, *Oryzopsis hymenoides*, *Elymus hystrix*, and *Bromus tectorum*. The soil is classified as a coarse-loamy, mixed, mesic Aridic Argixeroll. This is an alluvial fan soil that was mainly derived from granitic rocks. The soil consists of about 40 cm of loamy sand to gravelly loamy sand overlying a subsoil of about 50 cm of sandy loam. The underlying material to over 200 cm is loamy coarse sand.

The ATV community is at 1830 m elevation and includes the following vegetation: *Artemisia tridentata* ssp. *vaseyana*, *Purshia tridentata*, *Ribes* sp., *Chrysothamnus viscidiflorus*, *Stipa columbiana*, *S. occidentalis*, *Elymus hystrix*, and *Bromus tectorum*. The soil is classified as a coarse-loamy, mixed, frigid Ultic Argixeroll. This type of upland soil formed in a residuum from granodiorite and consists of about 60 cm of gravelly coarse sand and loamy coarse sand overlying a subsoil of about 30 cm of loamy coarse sand and sandy loam. The underlying material consists of about 10 cm of weathered granodiorite.

METHODS

Sampling was conducted on seven dates in 1989 and five dates in 1990. Four replicate macroplots (20 × 20 m) were randomly selected at each site. One shrub within a macroplot was selected for sampling each year. We changed shrubs to ensure that the prior year's sampling did not influence measured parameters. Within each macroplot a CR10 micrologger (Campbell Scientific, Logan, Utah)[3] was equipped to measure soil temperature at 10 cm and soil moisture at 10, 30, and 60 cm, adjacent to the target shrub. Soil temperatures were measured with thermocouples, and soil moisture with gypsum blocks. Leader length was measured as a plant growth indicator (Barker and McKell 1986) to avoid destructive harvest of *Artemisia* shrubs. Five marked leaders were measured on the target shrub within each macroplot at each sampling date.

Soil samples were collected with a spade to a depth of 20 cm from within the dripline of the target shrub in each macroplot on each date. Sample volumes were about 8000 cm^3 (20 × 20 × 20-cm cube). Roots were sieved from soil, and both root and soil samples were placed in plastic bags and kept on ice prior to

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[3] Mention of trade names does not indicate endorsement by USDA.

storage at –2°C. During the sieving process we discarded non-*Artemisia* roots, which are easily differentiated by color and morphology. In the laboratory roots were washed and cut into 1-cm segments; they were then cleared with KOH and stained with trypan blue (Phillips and Hayman 1970). We estimated percent total, arbuscular, hyphal, and vesicular colonization using the gridline-intersect method with a compound microscope at 160X.

Hyphal lengths were quantified using the following modified Bethlenfalvay and Ames (1987) procedure: (1) 20 g of soil was added to 100 ml of 0.05% trypan blue solution and boiled for 15 min; (2) samples were cooled and 100 ml of sodium hexametaphosphate was added to each flask; (3) flask contents were added to a Waring blender and blended for about 5 sec; and (4) an aliquot was added to a microscope slide and scored for hyphal lengths at 400X. Hyphal lengths were measured on six different aliquots per soil slurry using an improved Neubauer ultra plane counting chamber with a depth of 0.1 mm. Four randomly selected transects from each aliquot were scanned at 400X. Each scan was 7.9 mm long and 0.395 mm wide. From these dimensions the liquid volume scanned was calculated (3.12×10^{-4} ml/ scan). Slides were scanned and hyphal lengths quantified using an image analysis system. Aliquots were averaged prior to statistical analysis. We tried a 1:50 soil to extractant ratio initially, but found we had to use 1:10 because VAM hyphal lengths were low. The 1:10 extraction has been shown by Ingham and Klein (1984) to be adequate for measuring hyphal lengths. Since roots were removed before extraction, VAM hyphal lengths presented do not include rhizoplane hyphae. Inclusion of rhizoplane hyphae would no doubt elevate hyphal lengths; however, exclusion of roots allows a more accurate depiction of the hyphae that extend beyond the zone of phosphorus depletion around roots. Criteria for determining VAM fungi were similar to those established by Allen and Allen (1986). Most mycorrhizal hyphae are branched, have a knobby appearance, are aseptate, absorb trypan blue, and are about 3–10 μm in diameter.

Soil samples collected from each site were composited each year for soil chemical and physical analyses. Nitrate, NH_4^+, and SO_4^{-2} were extracted using 0.1 M KCl; phosphorus was extracted using sodium bicarbonate (Olsen and Sommers 1982); organic carbon was determined using the Walkley-Black procedure (Nelson and Sommers 1982); and particle-size analysis was determined using standard methods (Gee and Bauder 1982).

Data were analyzed by year. *Artemisia* sites and sampling date effects were assessed using analysis of variance with SAS (Statistical Analysis System). All VAM root colonization data were transformed by taking the arcsine and square root of VAM root intersects per total root intersects prior to conducting analysis of variance.

RESULTS

The ATT site had significantly higher levels of bicarbonate extractable P, KCl extractable SO_4^{-2}, and KCl extractable NO_3^- than the ATV site (Table 1). ATT soils had a significantly lower proportion of sand and significantly more silt and clay than ATV soils. Organic carbon and NH_4^+ were not significantly different between the two sites. Neither soil chemical nor physical characteristics were significantly different between years (Table 1). The significant Site*Date interaction for extractable P is evident since P increases in the second year at the ATT site, yet decreases at the ATV site.

Leader lengths were shorter in both plant communities in 1990 than in 1989 (Fig. 1). In addition, leader length was slightly higher in the ATV community in both years. Decreased leader lengths in 1990 are attributed to lower

TABLE 1. Means and probability values for soil physical and chemical characteristics of the *A. tridentata* ssp. *tridentata* (ATT) and *A. tridentata* ssp. *vaseyana* (ATV) sites in 1989 and 1990. Soil samples used for mycorrhizal characterization were used in this analysis, which accounts for the change in textural analysis between years. Inorganic P (bicarbonate extractable), N (KCl extractable), S (KCl extractable), and Walkley-Black soil organic carbon (O.C.) are given in the table ($n = 4^a$).

	ATT		ATV		
Soil variable	1989	1990	1989	1990	Site
% sand	84.2	80.4	91.1	92.3	.006
% silt	11.5	14.8	6.2	5.8	.008
% clay	4.3	4.9	2.8	1.8	.046
P $\mu g\ g^{-1}$	12.1	14.3	9.8	7.9	.0005
NH_4 $\mu g\ g^{-1}$	5.2	5.1	5.6	3.4	.39
NO_3-$\mu g\ g^{-1}$	6.6	8.3	4.6	4.0	.03
SO_4^{-2} $\mu g\ g^{-1}$	7.8	9.6	4.6	5.2	.001
O.C. mg g^{-1}	9.6	8.8	9.3	10.0	.62

[a] The effect of year was not significant ($P > .05$) for any variable, and only in the case of P was the Site and Year interaction significant ($P < .05$).

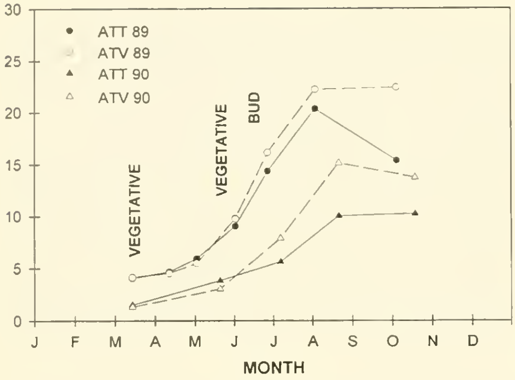

Fig. 1. Seasonal change in leader length for *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) during the 1989 and 1990 growing seasons. Phenological stage appears at the top of the graph.

precipitation received during that year (Fig. 2). Annual precipitation for the growing season was measured beginning in November. In 1989 ATT and ATV communities received 384 and 436 mm of precipitation, respectively. However, during 1990 the ATT and ATV communities received only 194 and 206 mm, respectively. The 4-year average precipitation (1984–87) for ATT and ATV was 211 and 256 mm, respectively.

The two sites were not different from each other in either maximum or minimum temperature (Fig. 2). Maximum March temperatures at 10-cm soil depths for both sites and years were 7–13°C, while minimum temperatures were 2–4°C. Maximum soil temperatures in July–August at 10 cm for both sites and years were 30–31°C, while corresponding minimum

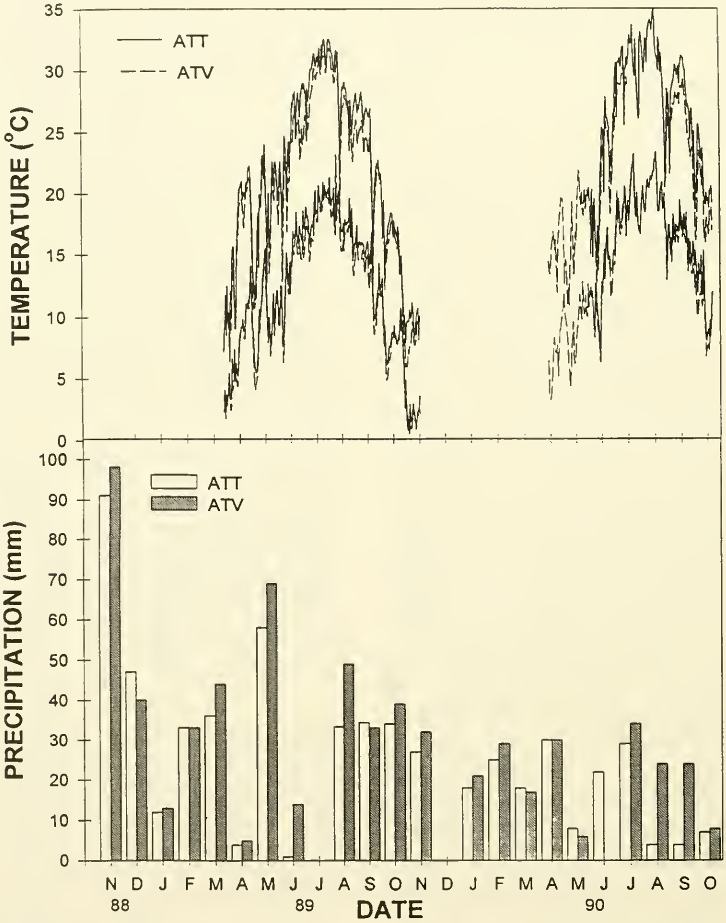

Fig. 2. Daily maximum and minimum soil temperatures at the 10-cm soil depth and monthly precipitation for *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) during the 1989 and 1990 growing seasons.

temperatures were 19–21°C. By mid-October maximum temperatures were 16–19°C and minimum temperatures were 8–9°C.

During early 1989 percent arbuscular colonization was similar for the two *Artemisia* subspecies but diverged to greater levels in ATV roots by early June (Fig. 3). Arbuscular colonization of ATT roots dropped to much lower levels than ATV roots during the midsummer dry period. This was followed by a minimal increase in colonization during fall for both subspecies. In 1990 percent arbuscular colonization was consistently lower for ATT than ATV roots (Fig. 4, Table 2). There was also a decrease in colonization from early spring through summer for both subspecies. Overall analysis of variance indicates a significant season and subspecies effect for percent arbuscular colonization in both years (Table 2).

In 1989 percent hyphal, vesicular, and total colonization did not significantly change through the season (Fig. 3, statistics in Table 2). However, in 1990 both percent hyphal and total colonization changed significantly through the season (Fig. 4, statistics in Table 2). In both years a significant subspecies effect was observed for vesicular and total colonization. Subspecies *vaseyana* roots had greater levels of colonization than *tridentata* roots.

Mycorrhizal hyphal lengths changed significantly through the season for both years (Fig. 5, statistics in Table 2). In 1989 and 1990 hyphal length more than doubled from March to May for all sites except the ATV site in 1990. Hyphal lengths decreased during summer and remained constant during fall for all sites with the exception of ATV in 1990, which increased slightly during the fall. Mycorrhizal hyphal lengths were significantly greater at the ATV site when compared to the ATT site for most sampling dates.

Soil moisture depletion data are presented in Figure 6. In both years the ATV site had higher soil water potentials for a greater proportion

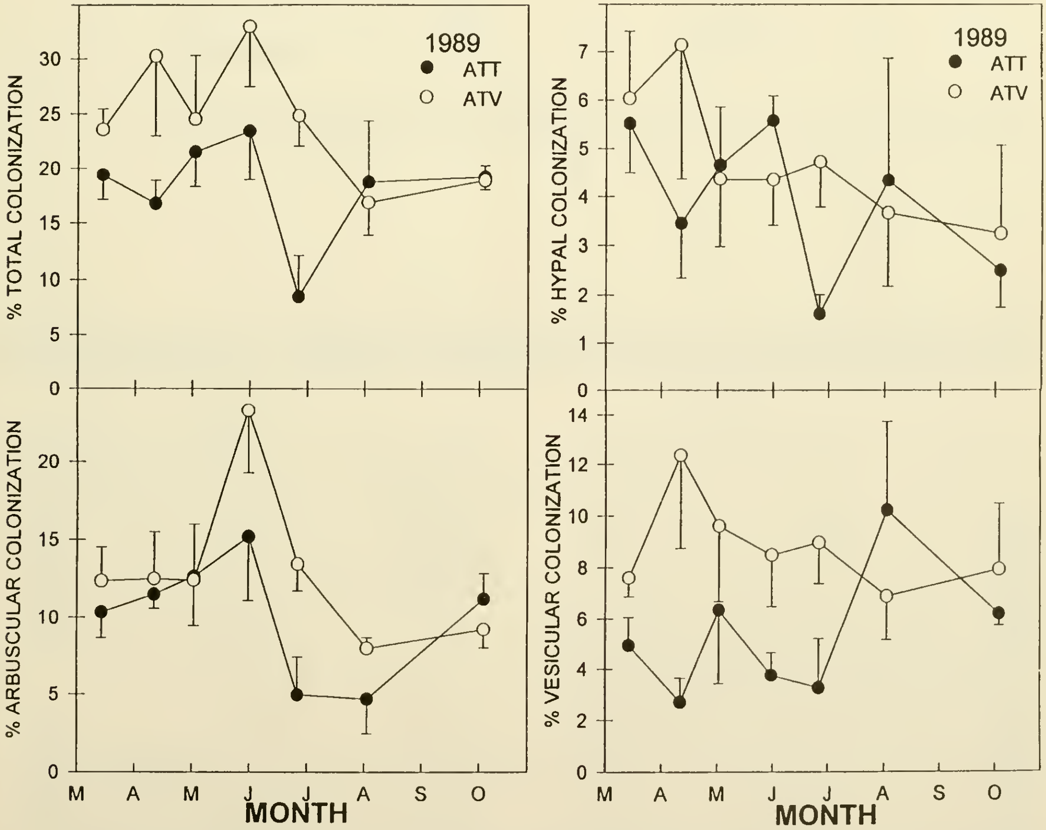

Fig. 3. Monthly changes in percent total, arbuscular, vesicular, and hyphal root colonization for *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) during the 1989 growing season.

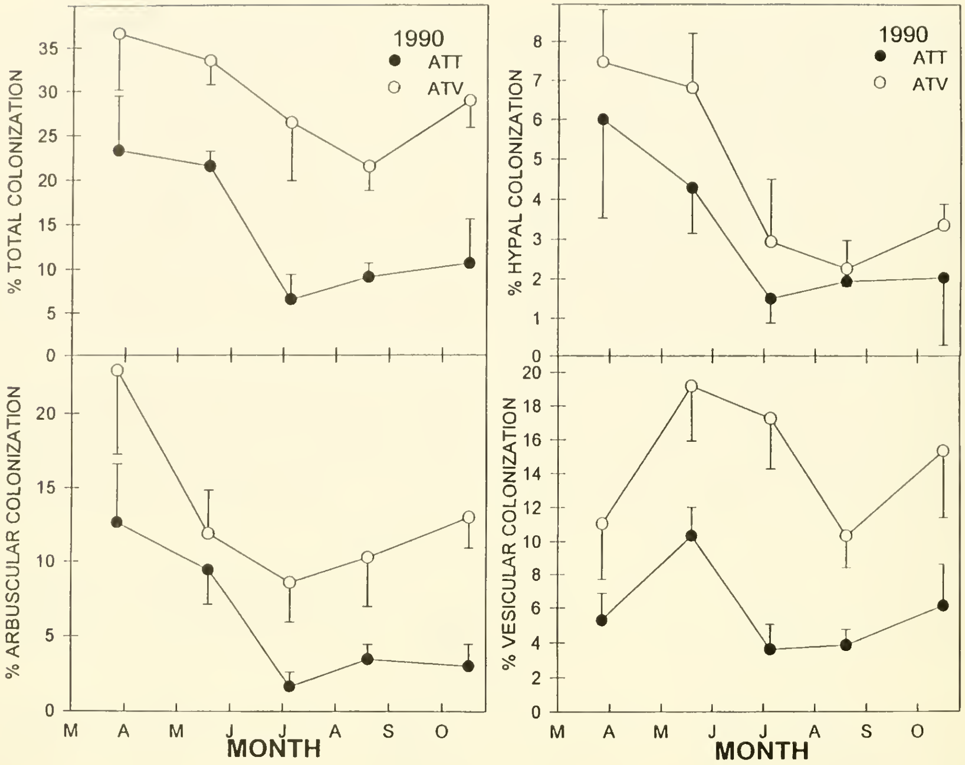

Fig. 4. Monthly changes in percent total, arbuscular, vesicular, and hyphal root colonization for *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) during the 1990 growing season.

TABLE 2. Site means and results of two-way ANOVAs showing the effect of sagebrush site (*Artemisia tridentata* ssp. *tridentata* vs. ssp. *vaseyana*) and time of year (Date) on mycorrhizal colonization (ARB = arbuscular colonization, VES = vesicular colonization, HYP = hyphal colonization, TOT = total colonization) and mycorrhizal hyphal length (mg^{-1}).

	Site means[a]		Probability values		
	ATT	ATV	Site	Date	Site*Date
			1989		
% ARB	10.1	13.1	.009	.014	.316
% VES	5.4	8.8	.004	.517	.031
% HYP	3.9	4.8	.346	.205	.563
% TOT	19.4	26.7	.004	.067	.149
Length	1.3	1.8	.018	.0004	.491
			1990		
% ARB	6.1	13.4	.0001	.005	.461
% VES	5.9	14.6	.0003	.116	.206
% HYP	3.1	4.6	.065	.003	.852
% TOT	15.1	32.6	.0001	.004	.511
Length	0.9	1.7	.005	.050	.373

[a] Site means were averaged over sampling date for each year (ATT = *Artemisia tridentata* ssp. *tridentata*, ATV = *Artemisia tridentata* ssp. *vaseyana*).

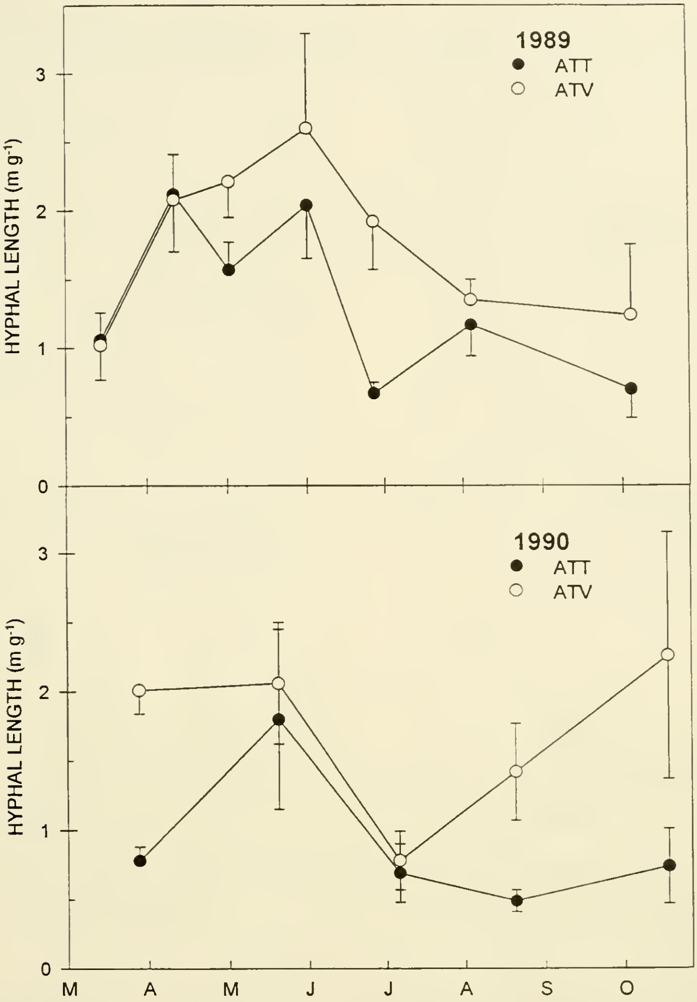

Fig. 5. Seasonal changes in mycorrhizal hyphal lengths (m of hyphae/g of soil) in soil adjacent to *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) during the 1989 and 1990 growing seasons.

of the season than did the ATT site. Soil moisture declined more rapidly in 1990 compared to 1989. Soil moisture at 10 and 30 cm fell below –1.5 MPa at both sites by midsummer 1990. In 1989 late summer and early fall precipitation raised soil water potentials above –0.2 MPa at both sites by October.

DISCUSSION

The two *Artemisia* subspecies exhibited consistent differences in both colonization and hyphal density of the associated mycorrhizae. Because the study was observational in nature, we could not separate genetics of two subspecies from the differences in sites they occupied. Thus, differences must be attributed to the species/site combination. The ATV site was slightly more mesic than the ATT site, but we did not detect any differences in temperature (Fig. 2). In general, ATV tends to occupy sites of higher elevation or with more summer precipitation than ATT (e.g., Winward 1980). In this study we also found that on a seasonal average the ATV site was lower in available nutrients than the ATT site (Table 1). Nutrient differences may be the result of either plant community differences or the fact that the ATV site had a higher sand content. Higher levels of colonization and greater hyphal lengths at the ATV site compared to the ATT site were thus associated with more available

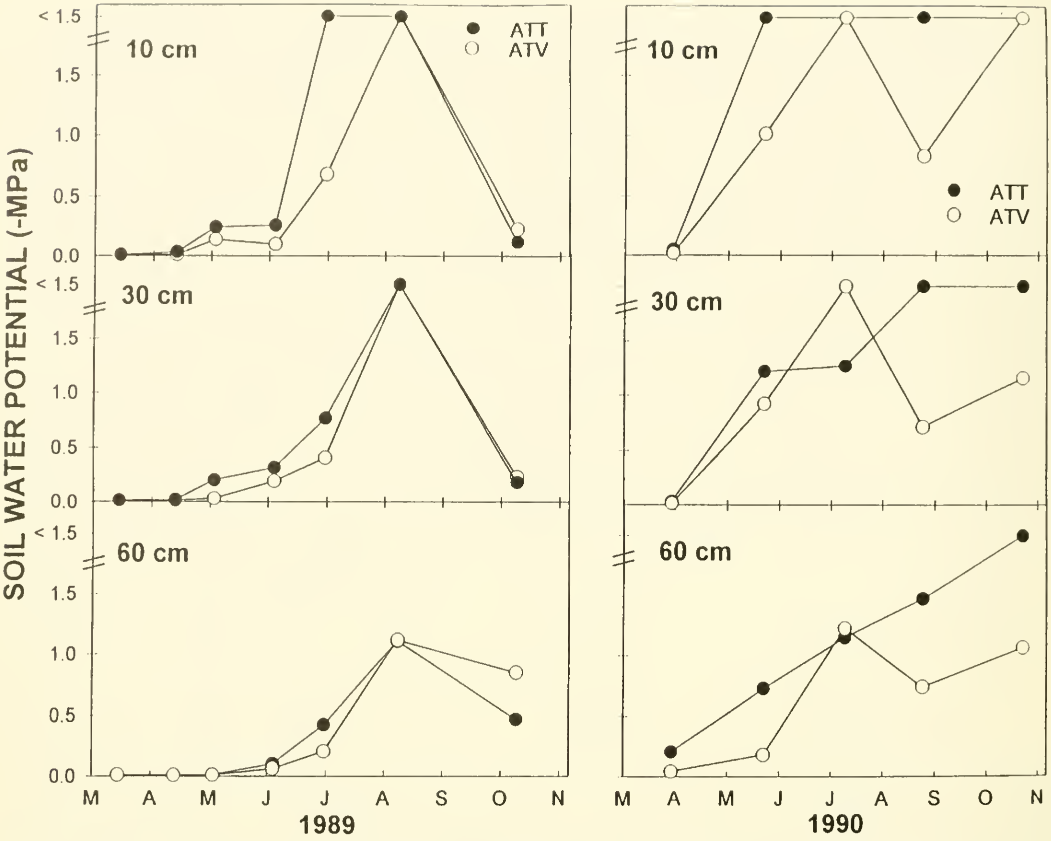

Fig. 6. Monthly change in soil water potential (–MPa) in *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) plant communities. Water potentials were measured in 1989 and 1990 at 10-, 30- and 60-cm soil depths with gypsum blocks.

soil moisture and lower nutrient availability. These data tend to support the hypothesis that mycorrhizae are more active when moisture is available and nutrients are limiting.

Arbuscular colonization is thought to be particularly important to carbon and phosphorus exchange (Cox and Tinker 1976, Wilcox 1993), and thus this feature plays a critical role in plant/fungus interaction (Hirrel et al. 1978, Chilvers and Daft 1982, Allen 1983). The two study sites differed in arbuscular colonization during both years. However, the difference was more consistent during 1990 compared to 1989. The difference in P availability between sites was 23% in 1989 and 81% in 1990. Thus, the greatest separation in mycorrhizal activity between sites corresponded to the greatest differences in P availability.

Timing of maximal mycorrhizal activity appeared to correspond to aboveground activity during the higher precipitation year of 1989. Previous research has demonstrated that *A. tridentata* achieves highest photosynthetic rates during late spring when moisture is available and temperatures are generally not limiting (DePuit and Caldwell 1973). The peak in root growth of *A. tridentata* also occurs in mid-April to late May (Fernandez and Caldwell 1975). Our measurements of leader growth (Fig. 1) appear to confirm that peak aboveground activity occurred in late spring or early summer during this study. However, during the dry year of 1990 there was no increase in mycorrhizal activity during the spring; rather, activity generally declined. The fact that precipitation and leader growth in 1990 were roughly half of 1989 values indicates that environmental stress may have limited plant activity in 1990. Plant stress and limited carbon assimilation likely reduced root and/or mycorrhizal activity. Because mycorrhizal activity can be a rather substantial carbon cost to the associated plant (Chapin et al. 1987), it is not surprising that mycorrhizal colonization and hyphal length would decline during a drought year.

Hyphal lengths appeared to be quite responsive to precipitation patterns within a year. Increases in hyphal lengths in the spring of 1989 were associated with spring precipitation. Hyphal lengths declined during the dry summer period and were stable during fall as both sites began receiving precipitation again. During 1990 hyphal lengths were stable during spring and declined during summer. In late summer and fall of 1990, the ATV site received precipitation and hyphal lengths increased (Figs. 5, 6). However, the ATT site did not receive significant precipitation and hyphal lengths did not increase. It appears that the pattern of arbuscular colonization more closely follows precipitation and hyphal lengths than does either vesicular or hyphal colonization. Arbuscular colonization and mycorrhizal hyphal lengths are more responsive to seasonal and yearly variations in plant growth than are either vesicular or hyphal colonization levels. We suggest, from a functional standpoint, that measurement of mycorrhizal hyphal length and arbuscular colonization is more relevant than is total colonization.

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SOIL AND VEGETATION DEVELOPMENT IN AN ABANDONED SHEEP CORRAL ON DEGRADED SUBALPINE RANGELAND

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ABSTRACT.—Vegetation and soils inside and outside an abandoned sheep corral on degraded subalpine range of the Wasatch Plateau were studied to determine the influence of approximately 37 years' use of the corral on soil and plant development. Vegetal and surface cover were estimated. Herbage, litter, and soils were sampled inside and outside the corral and analyzed for C_{org}, N, P, and S. Soil pH, bulk density, and CO_3-C also were measured. Storage (mass/unit area) of C_{org}, N, P, and S was determined for each component. Yield and vegetal composition were significantly affected inside the corral boundary. Herbage yield was 2.2 times greater, litter mass 16 times greater, foliar cover of grasses 2 times greater, and forb cover 70% lower inside than outside the corral. Cover of meadow barley (*Hordeum brachyantherum*), a component of the predisturbance vegetation of the Wasatch Plateau, was nearly 12 times greater inside than outside the corral. These and other vegetal and cover differences reflect inside-outside differences in concentration, storage, and availability of soil C_{org}, N, P, and S. Concentrations of C_{org} and total and available N, P, and S were greater in the surface 5 cm of soil inside the corral. Available P inside the corral was much higher in all soil layers. Because of bulk density differences, storage was greater inside the corral only for C_{org} and N at 0–5 cm and for P at 5–15 cm. Lower soil pH inside the corral appears related to soil P distribution and CO_3-C storage. Results suggest a need to reexamine earlier conclusions that tall forbs are the climax dominants of the Wasatch summer range.

Key words: summer range; soil C_{org}, N, P, S, CO_3-C, pH, and bulk density; plant composition and cover; biomass yield; litter.

After 35 years of destructive grazing by cattle and sheep in the late 1800s, the subalpine range of the Wasatch Plateau east of Ephraim, Utah, was in extremely poor condition (Reynolds 1911, Sampson and Weyl 1918, Sampson 1919). Erosion and alteration of vegetal cover reached such severe proportions that most of the soil A horizon was lost to erosion, and mud-rock floods were a common occurrence in the canyons leading to valleys and settlements at the base of the Wasatch Front (Reynolds 1911, Croft 1967). In some places only subsoils remained when control of grazing was finally achieved with establishment of the Manti National Forest in 1903 (Reynolds 1911, Sampson and Weyl 1918, Ellison 1949). Although condition of the range improved steadily over the next several decades, most of the summer range was still unstable in 1950, and accelerated erosion was continuing but at greatly reduced rates (Ellison 1954, Meeuwig 1960).

Under moderate grazing secondary succession occurred from 1903 to about 1940 when it slowed perceptibly (Ellison 1954). Since then succession has been extremely slow (Johnson 1964, Intermountain Research Station, Ogden, Utah, unpublished data). Our observations suggest that soil and vegetal conditions have essentially stabilized since Ellison's last observations in the mid-1950s. We believe the slow rate of succession and range improvement in the Wasatch subalpine since then is directly attributable to extreme amounts of soil loss and relatively low fertility of soils that remained after the period of degradation. Based on examination of numerous soil profiles on the plateau and those of similar soils elsewhere, we believe at least 50%, and possibly as much as 80 or 90%, of the A horizon was lost from this summer range via accelerated erosion. Such a loss would certainly remove a large portion of the soil's organic matter and nutrient capital and significantly alter productive potential.

In recent years we have pursued this hypothesis with several studies. This paper reports the results of a fortuitous observational study designed to demonstrate the effect of organic matter and nutrient additions over time on development of soils and vegetation of the Wasatch subalpine range. During field studies in 1988, we happened upon an abandoned and dilapidated sheep corral that obviously had not been used in many years (Fig. 1). No remains of manure were present inside the corral; vegetation and litter development were advanced and perennial grasses were abundant (Fig 2A). The contrast with vegetation and litter outside of what remained of the corral fence was striking (Fig. 2B).

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The corral offered an opportunity to document effects of use of the corral (1936–73) and inputs of organic matter and nutrients via sheep manure during its use to soil and vegetal development inside the corral boundary.

STUDY AREA

The Buck Ridge corral study site (39°15′N, 111°26′W) is located about 18 km east of Manti, Utah, on Cherry Flat adjacent to Buck Ridge Road and about 1.6 km east of Skyline Drive. This location is 5 km south of the Alpine Station and the well-known and studied Watersheds A and B of the Great Basin Experimental Range established by Dr. Arthur W. Sampson in 1912 (Sampson and Weyl 1918, Meeuwig 1960). Cherry Flat is typical of the crest of the Wasatch Plateau, which is about 3150 m elevation. The plateau is long, narrow, and oriented approximately north and south with riblike ridges extending east and west. The top of the plateau is gently rolling to nearly level. Average annual precipitation is about 840 mm; two-thirds of this falls as snow between November and April. Precipitation averages 173 mm during the summer months (June through September) but varies considerably. Mean annual temperature is about 0°C (Ellison 1954).

In the vicinity of the corral, Cherry Flat has a gentle 2% slope to the east; microtopography is smooth. Soil parent materials are of the Flagstaff Formation (Stanley and Collinson 1979) that crop out over about 7200 km^2 in central Utah (Schreiber 1988). Dominant lithology is freshwater lacustrine limestone and

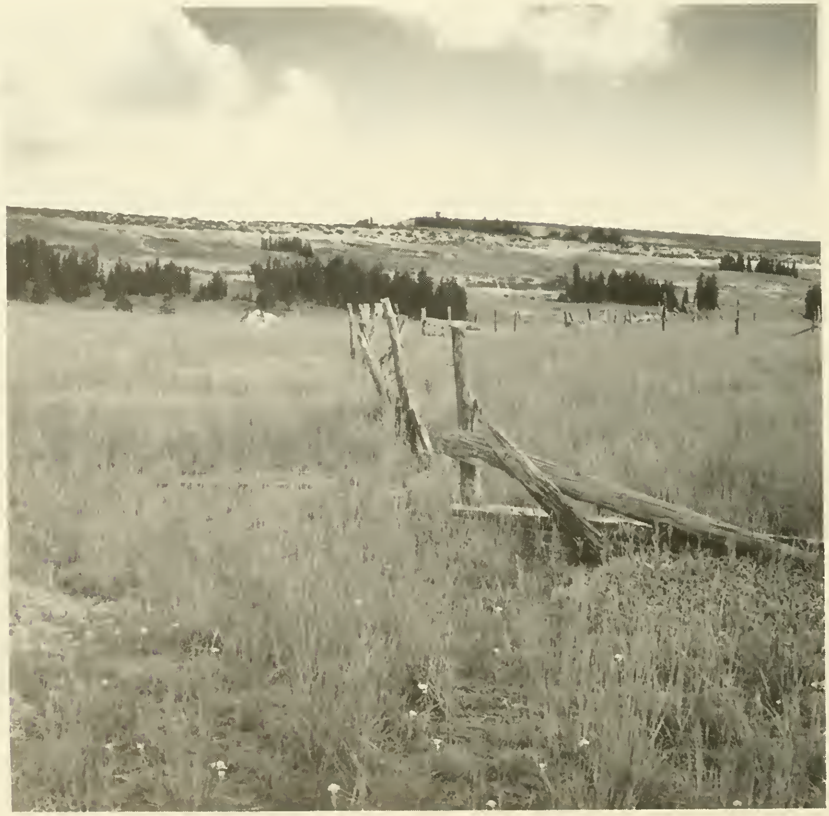

Fig. 1. Remains of Buck Ridge corral as it appeared in 1989.

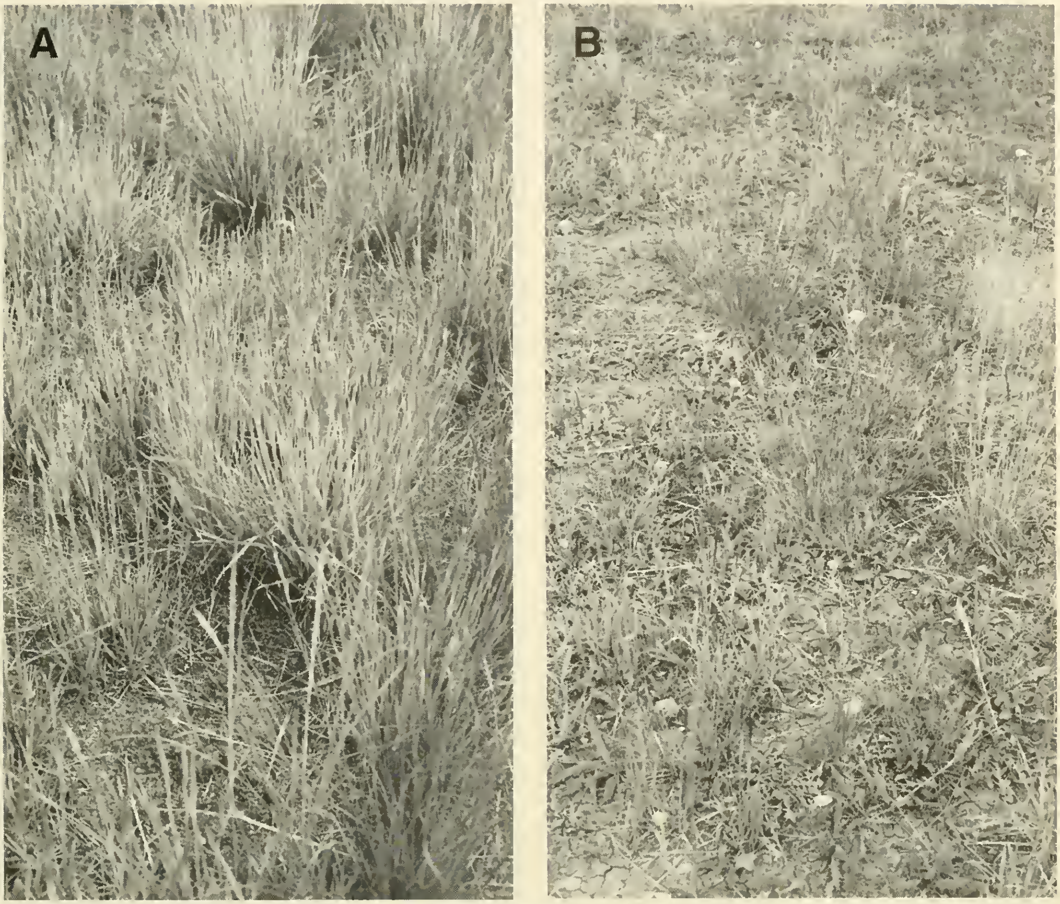

Fig. 2. Close-up view of vegetation and groundcover inside (A) and outside (B) Buck Ridge corral in 1989.

calcareous shales with minor interbeds of sandstone, oil shale, conglomerate, gypsum, and volcanic ash (Weber 1964, Schreiber 1988). Soils in this region of the plateau are mostly fine, mixed Argic Cryoborolls, but lithic, pachic, and vertic Cryoborolls also are present. They are shallow to moderately deep; the subsoils are silty clays or clay loams. Thickness of the A horizon averages about 4 cm; the B horizon averages approximately 52 cm thickness. Based on typical profile descriptions (H. K. Swenson, Soil Conservation Service, Boise, Idaho, personal communication), these relative horizon thicknesses suggest that much of the original A horizon was lost by wind and water erosion following the period of unrestricted grazing prior to 1903.

Vegetation of the Wasatch Plateau is chiefly herbaceous, but small patches of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) occupy steep northerly exposures of east-west ridges and dot the plateau landscape. Because there were no remnants of the original pristine vegetation (Ellison 1949, 1954), opinions differ regarding its exact character. Ellison (1954) describes the original plant community as mixed-upland herb dominated by tall forbs, while Sampson (1919) considered wheatgrasses to be the primary species of the herbaceous climax (i.e., what he referred to as summer range).

Based on file records and discussion with former permittees, we determined Buck Ridge corral was built and first used in 1936. It was last used about 1973 (Ed Shoppe, Manti-LaSal National Forest, Ephraim, Utah, personal communication). Hence, the corral was used annually by sheep for about 37 years. During this period undetermined and variable amounts of organic matter and nutrients were added annually via dung and urine, depending on the number and size of bands using the corral and frequency of use. For the past 10 years, the Buck Ridge allotment, comprising 4235 ac, has been grazed by sheep at the rate of 3.3 ac/AUM from 1 July to 30 September.

METHODS

As a basis for conducting this observational study, we first assured ourselves that areas inside and outside the corral boundary were initially alike in every respect and that site characteristics had no bearing on the precise location of the corral at the outset or on the findings. There were no differences in topography (or microtopography) and no evidence that other state factors (climate, biotic factor, parent material) differed within the small study site (about 0.75 ha) of the corral area. To assess the differential effect of nutrient additions inside and outside the corral, we sampled vegetation, litter, and soil in midsummer. Moisture conditions were dry at the time and little grazing had occurred inside or outside the corral. Present condition of the corral fence (Fig. 1) indicates that sheep have had near equal access to both sides of the corral boundary for many years, but there is no record of how long fence cross rails have been down.

Cover by species (foliar projection), litter, soil, and rock were estimated in 10 randomly located 0.5-m^2 plots inside and outside the corral (within 10 m of the corral boundary). Herbage and litter were harvested in the same plots, oven-dried (70°C), and weighed. Six randomly located soil pits were sampled inside and outside the corral. At each pit, soil cores (5.197 cm dia.) were collected from the 0–5-, 5–15-, and 15–30-cm layers. Plants and litter were ground to pass through a 0.425-mm sieve. Soils were air-dried, sieved to remove the >2-mm fraction, and then ground to pass through a 0.150-mm sieve.

Plant and soil samples were analyzed for total N by semi-micro-Kjeldahl (Bremner and Mulvaney 1982) and total S by dry combustion (Tiedemann and Anderson 1971) in a LECO high-frequency induction furnace (LECO Corp., St. Joseph, Michigan). Plant and soil samples were analyzed for total C by dry combustion (Nelson and Sommers 1982) in the LECO high-frequency induction furnace. Organic C (C_{org}) of soils was determined by correcting total C for carbonate-C as determined by a gasometric method (Dreimanis 1962). Total P was determined in plant material using the vanado-molybdo-phosphoric yellow color method after dry-ashing (Jackson 1958) and in soils using ascorbic acid color development (Olsen and Sommers 1982) following hydrofluoric acid digestion (Bowman 1988). Available nutrients in soils were determined as follows: P using ascorbic acid color development following 0.5 M sodium bicarbonate extraction (Olsen and Sommers 1982), N by steam distillation of 2 N KCl extracts (Keeney and Nelson 1982), and S with 1:1 water extracts, followed by ion chromatography (Dick and Tabatabai 1979).

Tests of significance for difference between inside and outside values for all variables studied were carried out with the *t* test. We recognize the desirability of replicating the inside-outside corral comparison. Unfortunately, that was not a design feature we could control; other abandoned corrals—even less than 37 years age—simply do not exist on this summer range.

RESULTS

Vegetation

Obvious visual differences in vegetation, litter, and soil surface conditions inside and outside the old corral (Figs. 2A, 2B) were confirmed in the data (Table 1). Herbage yield inside the corral was 2.2 times greater than outside. Although total herbage cover inside and outside the corral was the same (65%), grasses comprised a much greater percentage of foliar cover than did forbs inside than outside the corral. Three perennial grasses (*Agropyron trachycaulum, Hordeum brachyantherum*, and *Stipa lettermani*) dominated vegetal cover inside the corral (Table 2); outside the corral *A. trachycaulum* and *S. lettermani* were equally important, but *H. brachyantherum* was unimportant.

Forbs were represented by 7 species inside the corral and 11 species outside (Table 2). *Taraxacum officinale* and *Achillea millefolium* were the dominant forbs inside and outside the corral, but their cover outside was much greater than inside. No other forb species constituted more than 4% of the herbage composition.

Soil surface protection by litter differed markedly inside and outside the corral. Mass of litter inside the corral was 16 times greater

TABLE 1. Influence of long-term corral effects on vegetation, litter, and soil surface characteristics at Buck Ridge.

Component and attribute	Inside	Outside	Difference sign. at $P <$
Herbage yield (g m^{-2})	139 ± 21[a]	64 ± 9	.005
Litter mass (g m^{-2})	312 ± 78	19 ± 2	.005
Foliar cover (%)			
Grasses	55 ± 5	28 ± 5	.001
Forbs	11 ± 3	37 ± 8	.05
Total	66 ± 3	65 ± 7	NS
Basal cover (%)			
Litter	71 ± 4	18 ± 4	.001
Bare ground + rock	3 ± 2	25 ± 4	.005

[a] Mean ± standard error; $n = 10$.

than outside, while cover of litter was 4 times greater (Table 1). This is consistent with the 12-fold difference in bare ground between inside and outside locations. Only 2% of the soil surface was bare inside the corral.

NUTRIENTS

Concentrations of all nutrients studied were influenced by dung and urine accumulation inside the corral (Table 3). Nitrogen concentration was higher in the herbage, litter, and 0–5-cm soil layer, but lower in the 15–30-cm soil layer inside than outside the corral. Concentration of C_{org} was parallel to that of N for the litter and soil layers, while P concentration was higher inside than outside only for litter and the 0–5-cm soil layer (Table 3). Concentration of S was higher inside than outside only for the upper soil layer.

Storage (mass/unit area) of all four nutrients was significantly greater inside than outside the corral for herbage and litter components (Table 4). Amounts of C_{org} were greater inside the corral in the surface soil, but lower in the 15–30-cm soil layer. Storage of N was greater inside the corral in the 0–5-cm soil layer, while storage of P was greater inside the corral in the 5–15-cm soil layer.

Availability of P was much higher inside than outside the corral in all soil layers (Table 5). Availability of N and S was significantly higher ($P < .10$) inside the corral only in the 0–5-cm soil layer.

TABLE 2. Percentage of species composition (by foliar cover) of vegetation inside and outside Buck Ridge corral.

	Percentage	
	Inside	Outside
GRASSES		
Agropyron trachycaulum	8.2	10.3
Alopecurus pratensis		1.6
Bromus carinatus	4.0	
Hordeum brachyantherum	35.6	3.0
Poa pratensis		0.7
Stipa columbiana	0.4	
Stipa lettermani	30.4	26.5
Total grasses	78.6	42.1
FORBS		
Achillea millefolium	8.8	18.0
Androsace septentrionalis	0.3	0.3
Artemisia ludoviciana v. *incompta*		2.7
Aster foliaceus v. *canbyi*		2.4
Cymopteris lemmonii		0.2
Descurania richardsonii	0.9	0.1
Erigeron ursinus		2.6
Gilia aggregata		0.2
Lesquerella utahensis		2.1
Polygonum glandulosa	0.2	
Ranunculus inamoenus	0.3	
Rumex mexicanus	3.5	
Taraxacum officinale	7.4	29.2
Viola nuttallii v. *nuttallii*		0.1
Total forbs	21.4	57.9

DISCUSSION AND CONCLUSIONS

Development of vegetation and stabilization of the soil surface at Buck Ridge corral were indeed striking considering the slow pace of secondary succession of the Wasatch summer range from 1903 to 1940 (Ellison 1954, Meeuwig 1960) and the apparent lack of trend since 1940. Values for herbage production, litter mass, and cover data portray control of the soil surface inside the corral and are in marked contrast to conditions outside the corral and the surrounding summer range, which is still relatively unstable and subject to accelerated erosion. We believe the vegetation trend observed inside the corral has occurred within a relatively short time—no more than 20 years, assuming vegetal development did not commence until after abandonment of the corral. This is not to say that ephemerals did not occupy the corral annually between periods of use, only to be eliminated during use.

The large changes in vegetation and soil surface conditions are consistent with changes in nutrient status of the soil-plant-litter system

TABLE 3. Concentration of C_{org}, N, P, and S in components of the soil-plant-litter system inside and outside Buck Ridge corral.

Nutrient	Component		Inside	Outside	Difference sign. at $P <$
			------------- $g\ kg^{-1}$	-------------	
C_{org}	Herbage		447.4 ± 7.1[a]	433.0 ± 4.2	NS
	Litter		420.0 ± 8.3	448.9 ± 7.2	.025
	Soil,	0–5 cm	134.2 ± 17.6	45.6 ± 2.2	.001
		5–15 cm	34.8 ± 2.7	39.5 ± 1.4	NS
		15–30 cm	21.8 ± 2.5	36.4 ± 2.0	.005
N	Herbage		21.75 ± 0.75	15.50 ± 0.82	.001
	Litter		19.48 ± 0.83	11.77 ± 0.77	.001
	Soil,	0–5 cm	14.05 ± 1.95	3.39 ± 0.21	.001
		5–15 cm	2.99 ± 0.23	3.05 ± 0.10	NS
		15–30 cm	1.89 ± 0.17	2.73 ± 0.17	.005
P	Herbage		2.23 ± 0.10	2.22 ± 0.21	NS
	Litter		1.99 ± 0.12	1.47 ± 0.08	.001
	Soil,	0–5 cm	2.36 ± 0.22	1.61 ± 0.06	.01
		5–15 cm	1.70 ± 0.13	1.44 ± 0.08	NS
		15–30 cm	1.36 ± 0.13	1.39 ± 0.09	NS
S	Herbage		1.29 ± 0.04	1.22 ± 0.04	NS
	Litter		1.10 ± 0.07	0.96 ± 0.10	.05
	Soil,	0–5 cm	1.42 ± 0.18	0.88 ± 0.08	.025
		5–15 cm	0.69 ± 0.22	0.74 ± 0.11	NS
		15–30 cm	0.68 ± 0.11	0.71 ± 0.05	NS

[a] Mean ± standard error; $n = 6$.

over the life of the corral and subsequent to its abandonment (Crocker and Major 1955, Olson 1958, Blackmore et al. 1990). Unfortunately, much of the corral history (actual herd use, inputs of dung and urine, and character of vegetation that occupied the corral between periods of use by sheep) was not documented. However, changes in concentration and accumulation of nutrients inside the corral seem reasonable, based on what might be expected from traditional use of a subalpine corral by sheep for 37 years, experience from other grazed systems (Blackmore et al. 1990, Scholes 1990), and an understanding of the chemistry of the elements studied here. We can be confident that concentrations of soil C_{org} and N inside the corral have declined since abandonment and change in the biotic factor (Jenny 1941). However, whether a new steady state has been reached yet is conjectural (Jenny 1941, Tiedemann and Klemmedson 1986), even though observed concentrations of soil C_{org} and N are within the range for comparable undisturbed soils (Retzer 1956, Youngberg and Dyrness 1964).

Because C, N, P, and S are ubiquitous in soil organic matter and its precursors (Stevenson 1986), close association among these elements should be expected in components of the Buck Ridge soil-plant-litter system, especially between C_{org} and N because soil N is almost entirely organic (i.e., about 98%). On the other hand, because of certain dissimilarities in the chemistry of these four nutrients and differences among them in physiological separation into dung and urine pathways (C and P entirely via dung, N and S predominately via urine; Floate 1970, O'Connor 1981, Barrow 1987, Sagger, MacKay et al. 1990), certain differences in nutrient accumulation patterns can be expected.

Close association of C_{org} and N was apparent even in the 15–30-cm soil layer where concentration of C_{org} and N and amount of C_{org} were lower inside than outside the corral. Such an unexpected difference at this depth lacks explanation, certainly none related to corral effects. It is not consistent with the large differences in C_{org} and N in the litter and 0–5-cm soil layer where effects of the corral would be most expected. Parent material seems the most likely cause of this difference, but samples from the study site were uniform in CO_3-C and varied randomly in N, P, and S. However, limestone and shales are noted for spatial variation, even within very short

TABLE 4. Storage of C_{org}, N, P, and S in components of the soil-plant-litter system inside and outside Buck Ridge corral.

Nutrient	Component		Inside	Outside	Difference sign. at $P <$
			kg m^{-2}		
C_{org}	Herbage		0.064 ± 0.007[a]	0.028 ± 0.004	.001
	Litter		0.129 ± 0.032	0.009 ± 0.001	.005
	Soil,	0–5 cm	3.46 ± 0.17	1.84 ± 0.13	.001
		5–15 cm	4.44 ± 0.61	3.94 ± 0.25	NS
		15–30 cm	4.30 ± 0.62	6.44 ± 0.63	.05
		Soil total[b]	12.19 ± 1.29	12.22 ± 0.80	NS
	Total system		12.34 ± 1.27	12.25 ± 0.80	NS
			g m^{-2}		
N	Herbage		3.17 ± 0.27	1.03 ± 0.16	.001
	Litter		6.23 ± 1.68	0.23 ± 0.04	.001
	Soil,	0–5 cm	348 ± 16	138 ± 10	.001
		5–15 cm	379 ± 50	304 ± 17	NS
		15–30 cm	370 ± 46	485 ± 50	NS
		Soil total	1079 ± 96	927 ± 62	NS
	Total system		1115 ± 105	928 ± 152	NS
P	Herbage		0.33 ± 0.04	0.15 ± 0.03	.001
	Litter		0.66 ± 0.18	0.03 ± <0.01	.005
	Soil,	0–5 cm	63 ± 4	64 ± 3	NS
		5–15 cm	216 ± 30	145 ± 14	.10
		15–30 cm	231 ± 43	250 ± 32	NS
		Soil total	551 ± 70	460 ± 44	NS
	Total system		552 ± 70	461 ± 44	NS
S	Herbage		0.19 ± 0.02	0.08 ± 0.01	.001
	Litter		0.37 ± 0.11	0.02 ± <0.01	.01
	Soil,	0–5 cm	37 ± 2	35 ± 3	NS
		5–15 cm	90 ± 16	77 ± 14	NS
		15–30 cm	134 ± 25	128 ± 18	NS
		Soil total	261 ± 42	241 ± 33	NS
	Total system		262 ± 42	241 ± 33	NS

[a] Mean ± standard error; $n = 10$ for herbage and litter, 6 for soil components.

[b] 0–30 cm

distances (C. F. Lohrengel, Department of Geology, Snow College, Ephraim, Utah, personal communication). Of 23 rock samples from the near vicinity (4-km radius) classified by Schreiber (1988), P concentration ranged 31-fold, with a C.V. of 1.46. The sample highest in P content, an organic-rich shale, burned under a match flame.

Phosphorus is relatively immobile but should accumulate in soils over time where P inputs exceed removal in grazed herbage (Sagger, Hedley et al. 1990). This would characterize the situation in Buck Ridge corral with the large inputs of animal excreta from 1936 to 1973. Moreover, decomposition of this material should facilitate P mobility, especially after pulverization by hoof action (Bromfield and Jones 1970). Although urine and dung hydrolyze rapidly causing NH_4 to accumulate and pH to rise, nitrification quickly takes over and, in the case of urine, within days pH will drop below control levels (Doak 1952, During et al. 1973, Haynes and Williams 1992). Indeed the initial impact of decomposition of most plant materials is an increase in bulk pH (Williams and Gray 1974). However, products of organic decay are predominantly acid; hence, acidification eventually dominates. Those horizons or soil layers that contain the products of primary decomposition, in this case the litter and 0–5-cm layer (Table 6), will show the greatest acidity (Swift et al. 1979) and a tendency for enhanced solubility and mobility of P. Significantly lower carbonate-C of soil inside than outside the corral (Table 6) manifests increased soil acidity inside the corral. James Clayton (personal communication, Intermountain Research Station, Boise, Idaho) suggests the CO_3-C difference inside and outside the corral is reasonable, based on estimated H^+ supplied by nitrification of urea and organic matter decomposition over a period of 37 years.

TABLE 5. Concentration of available soil N, P, and S inside and outside Buck Ridge corral.

	N			P			S		
Soil Layer	Inside	Outside	Diff. sign. $P <$	Inside	Outside	Diff. sign. $P <$	Inside	Outside	Diff. sign. $P <$
	----- mg kg^{-1} -----			----- mg kg^{-1} ----			----- mg kg^{-1} ----		
0–5 cm	105 ± 26[a]	52 ± 11	.10	158 ± 19	57 ± 6	.001	50 ± 13	22 ± 3	.10
5–15 cm	29 ± 7	20 ± 3	NS	142 ± 16	22 ± 4	.05	24 ± 2	22 ± 1	NS
15–30 cm	13 ± 3	13 ± 2	NS	70 ± 11	10 ± 3	.001	15 ± <1	14 ± 1	NS

[a] Mean ± standard error; $n = 6$.

The P distribution pattern described here is similar to that found by Sagger, MacKay et al. (1990), who closely predicted observed P accumulation in soil of sheep pastures. In areas where sheep camped, 85–90% of P accumulated in the upper 15 cm of soil was accounted for by animal waste. Williams and Haynes (1992) noted significant increases of P in the top 20 cm of soil in pastures grazed by sheep for 38 years and treated with superphosphate.

Nitrogen and S losses from the corral soil-plant system could have been large. Nitrogen may be lost by volatilization of NH_3, leaching and surface runoff of NO_3, or denitrification under appropriate conditions (Ball et al. 1979, Floate 1981, O'Connor 1981), while SO_4 may be lost by surface runoff and leaching, depending on SO_4 retention capacity of soils (Sagger, Hedley et al. 1990). Williams and Haynes (1992) assumed most of the S loss they observed (48–73%) was due to leaching. Thus, whether Buck Ridge corral was devoid of vegetation during much of the year and hence subject to leaching and runoff, or whether its use was intermittent so as to permit vigorous growth of ephemerals and uptake of available nutrients, we would not expect mineralized N and S to accumulate in the soil profile.

Similarity in P and S accumulation in the 0–5-cm soil layer, in view of higher concentrations of these nutrients, is attributed to lower bulk density of the upper soil layer inside the corral (Table 6). By contrast, bulk density of the 5–15-cm layer was significantly greater inside than outside the corral. These opposite trends in adjacent soil layers appear to be due to compaction of the entire upper 15 cm during 37 years of use of the corral by sheep, followed by amelioration of this effect in the absence of trampling after the corral was abandoned, especially in the top 5 cm where organic matter was concentrated (Tables 3, 4). Heavy clay subsoils of this site should compact readily. Sommerfeldt and Chang (1985) found that long-term manure treatments reduced bulk density of the upper 15 cm of a cultivated soil by as much as 39%.

Increased availability of nutrients in the upper 5 cm of soil of the corral soil is associated with higher concentration of nutrients and the large pool of organic matter in that layer. Carbon/element ratios of all soil-plant components (Table 7) indicate that conditions generally more favorable for net mineralization of N and P (Stevenson 1986) prevailed inside than outside the corral at the time of sampling. Greater availability of P in all soil layers inside the corral also can be associated with pH in a range that one might expect maximum availability of the labile inorganic P fraction (Stevenson 1986). Coupled with this is low mobility of P, in contrast to N and S, which allows P to be retained in place.

Since abandonment of the corral, organic matter would have continued to accumulate, but from a new source, i.e., autotrophic production of vegetation that presumably developed soon after corral abandonment. Significant import of new nutrients since abandonment is unlikely. Almost all nutrients in post-abandonment crops of herbage would have been recycled from the soil. Presumably, the level of herbage production inside the corral has exceeded that outside almost since abandonment owing to higher fertility status of soils inside the corral. The present condition of the corral fence (Fig. 1) would indicate that it has not been a barrier to sheep for many years. Hence, differential grazing probably has played a minor role in vegetal differences inside and outside the corral boundary. Although we have emphasized the role of nutrients in the observed changes, we cannot dismiss the possibility that improvement in moisture-holding capacity of surface soils

TABLE 6. Effects of inside and outside positions of Buck Ridge corral on bulk density, pH, and carbonate-C of soil layers.

Soil property	Soil layer (cm)	Inside	Outside	Difference sign. at $P <$
Bulk density (mg m^{-3})	0–5	0.59 ± 0.08[a]	0.84 ± 0.06	.05
	5–15	1.26 ± 0.04	1.10 ± 0.02	.005
	15–30	1.39 ± 0.06	1.26 ± 0.10	NS
pH	0–5	6.58 ± 0.11	7.23 ± 0.13	.005
	5–15	7.15 ± 0.06	7.28 ± 0.09	NS
	15–30	7.17 ± 0.06	7.37 ± 0.09	.10
Carbonate-C concentration (g kg^{-1})	0–5	5.20 ± 0.82	8.92 ± 1.87	.10
	5–15	5.35 ± 1.24	9.23 ± 2.10	NS
	15–30	4.13 ± 0.94	10.63 ± 2.19	.05
amount (kg m^{-2})	0–5	0.15 ± 0.04	0.38 ± 0.10	.10
	5–15	0.65 ± 0.13	0.74 ± 0.17	NS
	15–30	0.77 ± 0.15	1.80 ± 0.36	.025
	Soil	1.57 ± 0.25	3.05 ± 0.54	.05

[a] Mean ± standard error, $n = 6$.

TABLE 7. Carbon-element ratios of soil-plant-litter components for inside and outside positons of Buck Ridge corral.

Ratio	Component	Inside	Outside	Difference sign. at $P <$
C/N	Herbage	19.6 ± 0.8[a]	30.7 ± 2.6	.05
	Litter	22.4 ± 1.0	37.2 ± 3.6	.05
	Soil, 0–5 cm	10.0 ± 0.2	13.3 ± 0.6	.001
	5–15 cm	11.7 ± 0.5	13.0 ± 0.5	NS
	15–30 cm	11.5 ± 0.6	13.4 ± 0.6	.05
C/P	Herbage	210 ± 15	241 ± 44	NS
	Litter	241 ± 23	308 ± 15	.05
	Soil, 0–5 cm	56 ± 5	29 ± 2	.001
	5–15 cm	21 ± 1	28 ± 2	NS
	15–30 cm	16 ± 1	27 ± 2	.025
C/S	Herbage	346 ± 16	368 ± 17	NS
	Litter	406 ± 43	439 ± 55	NS
	Soil, 0–5 cm	95 ± 5	54 ± 5	.001
	5–15 cm	53 ± 5	61 ± 11	NS
	15–30 cm	34 ± 3	53 ± 5	.01

[a] Mean ± standard error; $n = 10$ for herbage and litter, 6 for soil components.

inside the corral also may have influenced the successional trend following abandonment.

Comparison of basal cover data for Buck Ridge corral (inside and outside) with that portraying conditions in 1946 for six "relic natural areas" and four stands on Elk Knoll (Elk Knoll Research Natural Area), as described by Ellison (1954), is revealing (Table 8). Similarity between cover of litter, bare ground, and rock at Elk Knoll (3.2 km west-northwest of Buck Ridge corral) in 1946 and in 1989 and what we found outside Buck Ridge corral supports observations that successional trend has been virtually static in the last 40-odd years. Although Elk Knoll had been previously grazed, it has been protected from grazing, except for wildlife, from 1903 (Ellison 1954) to the present. According to Ellison, the natural areas, which he claimed had never been grazed by domestic livestock or had been grazed only lightly for many years, provided a partial description of pristine vegetation in the Wasatch subalpine at that time.

Vegetal cover data (Table 1) demonstrate a marked trend toward perennial grasses inside the corral. We interpret this as an upward

TABLE 8. Comparison of cover data for Buck Ridge corral with Ellison's data for "relic natural areas" and sites at Elk Knoll.

Location	Litter cover	Bare ground + rock
	- - - - - - - - - %	- - - - - - - - -
Buck Ridge corral		
Inside corral	71	3
Outside	18	25
"Relic natural areas"[a]	11–20	11–50
Elk Knoll		
1946[a]	26–31	29–37
1989[b]	27–49	17–39

[a] See Ellison (1954).

[b] Klemmedson and Tiedemann, unpublished data

trend in succession; vegetation changes are accompanied by greater herbage production, increased litter mass and cover, and stability of the soil surface. These characteristics have been commonly associated with improvement toward high range (ecological) condition (Laurenroth and Laycock 1989).

Interestingly, herbage composition inside the corral is in marked contrast to that described by Ellison (1954) for his six relic natural areas. He said that "one of the most striking things about the natural areas is the abundance of perennial forbs"; they constituted 70–88% of the vegetation in relic natural areas in 1946. The trend toward perennial grasses (79% of total foliar cover) we have observed inside the corral is quite the opposite of Ellison's composition data and corresponds more to vegetation development of the summer range described by Sampson (1919). The increase in *Hordeum brachyantherum* also suggests an upward trend. Both Ellison (1954) and Sampson (1919) noted the presence of *H. nodosum*, a synonym misapplied to *H. brachyantherum* (Hitchcock 1950, Holmgren and Reveal 1966), on the summer range. But only Sampson (1919) discussed successional status; he described *H. nodosum* as a shallow-rooted species that occupied space between bunched wheatgrasses, the primary species of the subclimax type. He did not list this plant with types of lower developmental stage.

Normally where ecosystem degradation has been as severe as experienced here, with almost complete loss of the A horizon, we would expect successional processes in soil and vegetation to occur simultaneously (Sampson 1919, Crocker and Major 1955, Olson 1958). But, in this case where livestockmen controlled the input of manure and associated effects for 37 years, ecosystem development was essentially one-sided; soil development advanced rapidly for 37 years before sheep use of the corral ceased and development of vegetation was allowed to proceed. The fact that development in vegetation, litter, and soil surface conditions has advanced so far in just 20 years, far outpacing comparable development outside the corral, even in Ellison's "relic natural areas," leads us to conclude that soil fertility has been a key factor controlling succession and improvement of the Wasatch summer range.

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GEOSTATISTICAL ANALYSIS OF RESOURCE ISLANDS UNDER *ARTEMISIA TRIDENTATA* IN THE SHRUB-STEPPE

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ABSTRACT.—Desert plants can influence the pattern of resources in soil resulting in small-scale enriched zones. Although conceptually simple, the shape, size, and orientation of these "resource islands" are difficult to study in detail using conventional sampling regimes. To demonstrate an alternative approach, we sampled soil under and around individual *Artemisia tridentata* (sagebrush), a dominant shrub of cool desert environments, and analyzed the samples with univariate statistics and geostatistics. Univariate statistics revealed that soil variables like total inorganic-N, soluble-C, and microbial biomass-C were distributed with highest mean values within about 25 cm of the plant axis and significantly lower mean values at distances beyond 60 cm. However, such simple analyses restricted our view of resource islands to identically sized, symmetrical accumulations of soil resources under each plant.

Geostatistics provided additional information about spatial characteristics of soil variables. Variography revealed that samples separated by a distance of less than about 70 cm were correlated spatially. Over 75% of the sample variance was attributable to spatial variability. We modeled these spatial relationships and used kriging to predict values for unsampled locations. Resulting maps indicated that magnitude, size, and spatial distribution of soil resource islands vary between individual plants and for different soil properties. Maps, together with cross-variography, further indicate that resource islands under *A. tridentata* are not always distinguishable from the surrounding soil by sharp transition boundaries and may be asymmetrically distributed around the plant axis.

Key words: resource islands, geostatistics, Artemisia tridentata, *nutrient availability, kriging, spatial correlation.*

Recognition that individual plants can significantly affect the local soil environment dates back to at least the middle of the nineteenth century (see Zinke 1962) and has been documented for many plant forms including broadleaf and coniferous trees (Zinke 1962, Everett et al. 1986, Doescher et al. 1987, Belsky et al. 1989), bunch grasses (Hook et al. 1991), herbaceous legumes (Halvorson et al. 1991), and, in particular, desert shrubs (e.g., Fireman and Hayward 1952, Garcia-Moya and McKell 1970, Nishita and Haug 1973, Barth and Klemmedson 1978, Burke 1989, Burke et al. 1989, Virginia and Jarell 1983, Bolton et al. 1990, 1993). Soil associated with plants typically contains greater concentrations of limiting resources (e.g., N, P), contains larger populations of soil microorganisms, and exhibits higher rates of nutrient cycling processes like mineralization (Charley and West 1977, Bolton et al. 1990) and denitrification (Virginia et al. 1982). These small-scale enriched zones, variously termed "fertile islands" (Garner and Steinberger 1989), "isles of fertility" (West 1981, Whitford 1986), "resource islands" (Reynolds et al. 1990), or "ecotessara" (Jenny 1980), are hypothesized to result from several mechanisms (Garner and Steinberger 1989), including litter-fall or stemflow (Zinke 1962), decreased erosion or increased deposition (Coppinger et al. 1991), microclimatological amelioration of the soil (Smith et al. 1987, Pierson and Wight 1991), or inputs of resources via insects, birds, or animals (Davidson and Morton 1984).

Detailed knowledge of the size and internal dynamics of resource islands is important for understanding energy flux, mass transport, and nutrient cycling processes at the scale of the individual plant. Resource islands may also connote a tier in a progressive, hierarchical mosaic of plant and animal habitats, resource distributions, and biogeochemical processes (i.e., patches sensu Kotliar and Wiens 1990). Estimates of the distribution and numbers of resource islands in the landscape may aid in understanding population level processes and can be used to refine regional estimates of energy flow and mass transfer. Furthermore, interrelationships of large numbers of individual resource islands may influence ecosystem structure, function, and stability (Reynolds et al. 1990, Schlesinger et al. 1990, Halvorson et al. 1991).

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Although conceptually simple, the size, shape, and orientation of resource islands are not easy to evaluate. Previous studies have typically been based on relatively small numbers of samples collected using a binary regime (i.e., samples collected beneath the plant versus samples collected "away" from the plant) or along a transect passing from plant to bare soil. Such an approach cannot be used to provide a detailed spatial analysis of resource concentrations or processes in the soil that are likely to exhibit complex responses to landscape and microsite variations (Burke et al. 1989). Additionally, data collected from different locations (or depths) have often been analyzed using inferential statistics such as ANOVA or *t* tests that assume samples are spatially independent and identically distributed. However, these assumptions may be dubious, if untested, since ecological phenomena are often spatially or temporally correlated and their frequency distributions are rarely normal (Rossi et al. 1992). Recently, a branch of applied statistics, known as geostatistics, has been demonstrated to be useful for determining spatial correlations among ecological data and for estimating values at unsampled locations (e.g., Robertson 1987, Robertson et al. 1988, Rossi et al. 1992).

Objectives of this study were (1) to use geostatistics to describe and model the spatial continuity of soil variables around individual plants, (2) to use this information to produce graphical representations or maps of specific resource islands, and, finally, (3) to quantify the spatial correlation between plants and soil variables. We examined *Artemisia tridentata* (sagebrush), a prominent shrub of cool desert environments (West 1983) previously known to affect the distribution of resources in the soil. Several workers have measured higher concentrations of resources such as total-C, total-N, inorganic-N, and higher rates of N cycling in soil beneath *A. tridentata* than in nearby open soil using a binary sampling regime (e.g., Burke 1989, Burke et al. 1989, Bolton et al. 1990, 1993). However, these studies have not accounted for possible spatial autocorrelation of the samples, evaluated resource islands of individual plants, nor quantified the scale of soil heterogeneity beneath *A. tridentata*.

Geostatistics has previously been used to describe environmental and soil parameters associated with *A. tridentata*. For example, Pierson and Wight (1991) used one-dimensional geostatistics to analyze spatial and temporal variability of soil temperature under *A. tridentata*. Halvorson et al. (1992) demonstrated that geostatistics was an appropriate means of measuring resource islands at the scale of an individual *A. tridentata* plant. Jackson and Caldwell (1993a) attempted to quantify the scale of nutrient heterogeneity around individual *A. tridentata* and *Pseudoroegneria spicata* in a native sagebrush steppe using semivariograms. They demonstrated increasing autocorrelation of soil nutrients at spatial scales <1 m but did not determine whether small-scale effects were attributable to individual plants or an artifact of the nested sampling design used. More recently, they constructed kriged maps that showed relatively high concentrations of soil variables like soil organic matter, extractable phosphate, and potassium near *Pseudoroegneria* tussocks but not *Artemisia* shrubs (Jackson and Caldwell 1993b). However, these kriged maps did not directly quantify spatial covariation between locations of individual plants and resource islands. Further, Jackson and Caldwell did not observe autocorrelation for microbial processes at any scale that was measured.

To meet our objectives, we applied geostatistics in three steps. First, we characterized and modeled the similarity between samples as a function of their separation distance and direction. Second, we used this relationship to interpolate values at unsampled locations directly under and near individual plants. Finally, we quantified spatial covariation between soil properties and plants.

STUDY SITE

The study was conducted at the Arid Land Ecology (ALE) Reserve, located on the Hanford Site in south central Washington (see Bolton et al. 1990 for details). There, remnants of the native *Artemisia tridentata–Elytrigia spicata* association occur on silt loams of the Warden or Ritzville series. This perennial shrub-steppe is the largest grassland-type in

North America and covers more than 640,000 km^2 of the Intermountain Pacific Northwest too dry to support forests (Daubenmire 1970, Rogers and Rickard 1988). In an undisturbed state the *A. tridentata–E. spicata* association would be composed typically of three layers of vegetation: an overstory shrub (*Artemisia tridentata tridentata*), a large caespitose perennial grass (*Elytrigia spicata* [formerly *Agropyron spicatum*]), and a small caespitose perennial grass (*Poa secunda*) growing on soil with a thin cryptogamic crust (Daubenmire 1970). However, following disturbance such as tillage, grazing, or fire, the alien annual grass *Bromus tectorum* becomes established.

METHODS

Soil Collection and Analysis

Cores of surface soil (10.5 cm dia. × 5 cm deep) were collected at 41 specific locations within 2 × 2-m plots centered on mature *A. tridentata* individuals (Fig. 1). Samples were located so as to minimize the number of data points needed for analysis of spatial characteristics and to avoid preferential clustering. We sampled five identically oriented plots (205 points) in March 1991, when levels of soil moisture and microbial biomass activity were high. All plots were located within approximately 20 m of each other within a flat area with randomly spaced plants. Multiple plots were sampled for two reasons: first, to assess spatial characteristics of resource islands by basing our calculations on several examples rather than a single instance; and, second, to provide replicates in the event that no spatial dependence of soil properties was observed. Data from all plots were combined to consider spatial dependence of soil properties around several *A. tridentata* plants simultaneously. This approach was chosen because it provided a more generalized evaluation of resource islands under individual *A. tridentata* and greatly increased the number of data pairs at any separation distance.

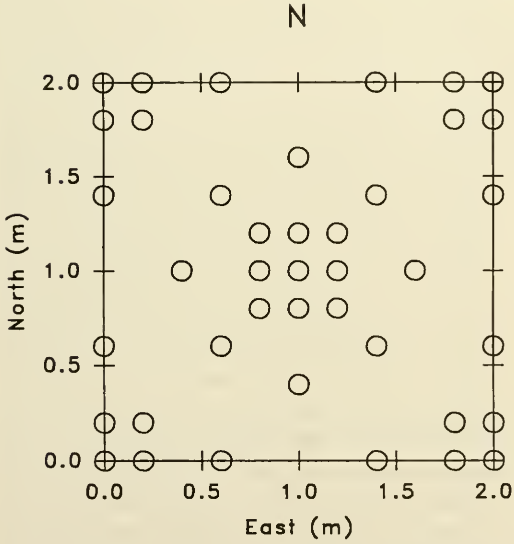

Fig. 1. Schematic of a typical sampling plot. Each plot (five total) was centered on an *Artemisia tridentata* plant. Dashed circles show the location of 41 soil cores (10.5 cm dia. × 5 cm deep). All five plots were oriented as shown.

Estimates of plant location were required for cross variography (see below). Therefore, vegetation maps were produced from vertical photographs. Each plot was divided into 5 × 5-cm squares. Each square was classified into one of three groupings—bare, grass species, or *A. tridentata*—based on predominant coverage. For this work no attempt was made to distinguish among grass species.

Each soil sample was sieved (5 mm), mixed, and analyzed for a variety of soil variables. For this work we present data only for water-soluble forms of C, total inorganic-N (i.e., nitrate + ammonium), and soil microbial biomass-C. Soluble soil C (H_2O-C) was extracted with room temperature deionized water and analyzed using an infrared gas analyzer (Ionics Inc., Watertown, Massachusetts). Total inorganic nitrogen (TI-N) was extracted within 48 h of collection from 10-g subsamples of soil using 25 ml 2M KCl and analyzed colorimetrically (Alpkem Corp., Clackamas, Oregon). Soil microbial biomass-C (SIR-C) was estimated from the respiratory response of soil to glucose, a source of C readily utilized by heterotrophic soil microorganisms (Anderson and Domsch 1978). Ten-gram samples of soil were placed in 40-ml glass vials, moistened with deionized H_2O, covered with Parafilm, and incubated in the dark at 23.5 ± 0.5°C for 1 wk. Each sample was then amended with a glucose solution at the rate of 600 mg glucose (240 mg C) kg^{-1} soil, bringing the final H_2O content of the soil to 20–25% (w/w; equivalent to 30–50 kPa). Glass vials were sealed with silicone septa and incubated for 3 h. Soil respiration was measured by gas chromatography and related to estimates of soil microbial biomass-C with equations developed by Anderson and Domsch (1978).

Univariate Statistics

Univariate statistics were calculated for each soil parameter. For classical inferential statistics, data were also assigned to one of five distance classes depending upon sample location within a plot. These classes can be envisioned as concentric rings located at increasing distances from the center of the plot. The first distance class comprised samples collected directly under *A. tridentata* (distance = 0 cm, *n* = 1 per plot), followed by the second (approximate distance = 25 cm, *n* = 8 per plot), third (approximate distance = 60 cm, *n* = 8 per plot), fourth (approximate distance = 110 cm, *n* = 12 per plot), and fifth (approximate distance = 130 cm, *n* = 12 per plot). Average values of soil properties in each distance class were plotted as a function of radial distance from the plant axis. Following variography (see below), $\log_{10}$ transformed samples deemed spatially independent were compared with ANOVA using plot as a blocking factor.

Geostatistics

VARIOGRAPHY.—We evaluated spatial characteristics of each soil parameter with the nonergodic autocorrelation function (Srivastava and Parker 1989) and summarized results graphically as correlograms. Like variograms, correlograms represent the average degree of similarity between samples as a function of their separation distance (lag) and direction. Unlike the variogram, the correlogram filters out the effects of changes in both lag means and lag variances. Each point in a correlogram was calculated from this equation:

$$\rho^*(h) = \frac{1}{N(h)} \cdot \frac{\sum_{i=1}^{N(h)} \{[z(x_i) - m_{-h}][z(x_i+h) - m_{+h}]\}}{S_{-h}\, S_{+h}} \qquad (1)$$

where $z(x_i)$ and $z(x_i + h)$ are two data points separated by the distance (lag) h. Datum $z(x_i)$ is the tail and $z(x_i + h)$ is the head of the vector, N(h) is the total number of data pairs separated by lag h, m_{-h} and m_{+h} are means of the points that correspond to tail and head of the lag, respectively, and S_{-h} and S_{+h} are standard deviations of tail and head values of the lag, respectively. We chose the correlogram because it removes the effects of lag means and standardizes by the lag variances (Rossi et al. 1992). For this work we express correlograms in the form of a standardized variogram by subtracting each $\rho^*(h)$ from 1 (Isaaks and Srivastava 1989, Rossi et al. 1992).

Correlograms were first calculated solely as a function of lag distance (i.e., the omnidirectional case) without considering any differences in spatial continuity with direction (i.e., anisotropy). However, since resource islands need not be symmetric (e.g., Zinke 1962), we also calculated directional correlograms. For each soil property a separate correlogram was calculated for samples oriented 0°, 45°, 90°, and 135° (±15° tolerance) from each other. Since correlograms are symmetric about the origin (i.e., 0° = 180°, 45° = 225°, etc.), 0°, 45°, 90°, and 135° directions correspond to samples aligned along east-west, northeast-southwest, north-south, and northwest-southeast axes.

Because the data of each plot were concatenated during this analysis, local anisotropies (i.e., anisotropies specific to each plot) were in effect combined. Thus, any directional effects we observed were a composite of the five plots and presumably indicative of overall directional trends. To identify directions of maximum and minimum continuity, we estimated the lag distance corresponding to a common value for each directional correlogram (Isaaks and Srivastava 1989). The directional correlogram with the greatest lag associated with a correlogram value of 1 was identified as the direction of greatest continuity. The correlogram with the smallest lag corresponding to 1 was deemed the direction of minimum continuity.

The empirically determined scatter of data points in each correlogram was fit with models known to produce a positive definite kriging system (i.e., matrices that provide both a unique solution and a positive estimation variance; Isaaks and Srivastava 1989). Such models typically contain several salient features known as nugget, range, and sill. The **nugget** is the amount of variance not explained or modeled as spatial correlation. It is the *apparent* ordinate intercept and is due to (1) unsampled correlation below the smallest lag and (2) experimental error (Rossi et al. 1992). A small nugget relative to the sill indicates that a large proportion of the sample variability is modeled as spatial dependence. Conversely, a large nugget indicates less sample variability can be modeled as spatial dependence. The sill is characterized by a leveling off of the correlogram model. If present, it indicates that spatial correlation is, on average, constant. However, if spatial correlation continues to change at lags greater than those considered in the correlogram, then a sill will not be apparent. The lag value when the correlogram model reaches the sill is known as the range. It represents the maximum separation distance within which samples are spatially correlated. At lags ≥ the range, the sill of the variogram may approach the sample variance (Barnes 1991).

KRIGING TO ESTIMATE DATA AT UNSAMPLED LOCATIONS.—Kriging has been likened to "multiple linear regression with a few twists" (Rossi 1989). In classical multiple linear regression, an estimate of the dependent variable, Y, is calculated from a weighted linear combination of independent variables where each is measured at about the same location in time or space. Usually, only a single value of Y is estimated. Similarly, in kriging, $z^*(x_o)$, the estimated value of the variable for an unsampled location (x_o), is calculated as a weighted linear combination of the surrounding sampled neighbors:

$$z^*(x_o) = \sum_{i=1}^{N} g_i \cdot z(x_i) \qquad (2)$$

where the $z(x_i)$'s are the sampled values at their respective locations, and the g_i's are the weights associated with each sample value. In ordinary kriging, weights used to estimate $z^*(x_o)$ are chosen so that the resulting estimate is unbiased and has a minimum estimation variance and sum to unity. Kriging incorporates a model of spatial continuity (here the correlogram model) and accounts for the degree of clustering of nearby samples and their distance to the point being estimated (Isaaks and Srivastava 1989). We used ordinary point kriging to estimate values of soil properties at unsampled locations. For each plot we estimated values for the nodes of a 5 × 5-cm^2 grid. Each predicted value was based on a minimum of 6 and a maximum of 12 neighbors located within a 0.8-m circular search radius.

CROSS-VARIOGRAPHY.—In addition to spatial characteristics of single soil properties, we also determined how soil properties covaried with plants. We modeled spatial covariation with $\rho^*_{AB}(h)$, the estimated nonergodic cross-correlogram. Like the correlogram, it accounts for both variables' fluctuating lag means and variances (Isaaks and Srivastava 1989, Rossi et al. 1992). Because comparisons between continuous variables (i.e., TI-N, SIR-C, and H_2O-C data) and discrete variables (i.e., plant data) might be complicated by a "contact effect" (Luster 1985), we converted TI-N, SIR-C, and H_2O-C data to binary variables using an indicator transformation (Journel 1983). For this work, continuous data values of TI-N, SIR-C, and H_2O-C were coded 1 if they were greater than the local (within-plot) median, or 0 following Halvorson et al. (in review). Cross-correlograms were then calculated for grass species or *A. tridentata* and indicator transformed TI-N, SIR-C, and H_2O-C data using the equation,

$$\rho^*_{AB}(h) = \frac{1}{N(h)} \cdot \frac{\sum_{i=1}^{N(h)} \sum_{k=1}^{N(h)} [I_A(x_i, z_A) - m_{A_{-h}}][I_B(x_k, z_B) - m_{B_{+h}}]}{S_{A_{-h}} S_{B_{+h}}} \qquad (3)$$

where N(h) is the total number of data pairs separated by vector h, $I_A(x_i, z_A)$ is the coded plant data (equal to 1 if the specified plant type was present or 0 if absent) at some location (x_i), $m_{A_{-h}}$ and $S_{A_{-h}}$ are the mean and standard deviation, respectively, for the plant variable at those data locations that are –h away from a soil property data location. Similarly, $I_B(x_k, z_B)$ is the coded soil variable data (equal to 1 if the data value is greater than the local plot median or else 0) at location (x_k), $m_{B_{+h}}$ and $S_{B_{+h}}$ are the mean and standard deviation of the soil variable indicator calculated for those locations that are +h away from a plant variable data location. Note, when h is 0, equation 3 is equivalent to the Pearson correlation coefficient (Isaaks and Srivastava 1989).

Unlike the correlogram, values calculated for the cross-correlogram may not be symmetric about the origin because both the order and direction are switched when variables are reversed (Isaaks and Srivastava 1989). Consequently, we calculated individual cross-correlograms for the 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315° directions (±30° tolerance). These correspond to soil samples aligned to the east, northeast, north, northwest, west, southwest, south, or southeast of a plant.

RESULTS

Summary statistics indicated that samples of TI-N and H_2O-C were positively skewed, while samples of SIR-C were more normally distributed (Figs. 2A–C). Total inorganic-N ranged from 0.6 mg / kg soil to a maximum of 23.6 mg / kg soil (Fig. 2A). The mean value for TI-N of 3.8 mg / kg soil compared reasonably to the values reported by Bolton et al. (1990) of 4.1 and 4.9 mg / kg soil for open soil crust and *A. tridentata* soil, respectively. Values observed for H_2O-C ranged widely from 9.8 mg / kg soil to 633.9 mg / kg soil (Fig. 2B). Estimates of SIR-C ranged from less than 200 to over 1800 mg / kg soil (Fig. 2C). The average value for SIR-C, 750 mg/ kg, was within the range reported by Burke et al. (1989) and equivalent to about 980 kg C / ha soil assuming a bulk density of 1.3 (Bolton et al. 1990). Comparatively, Smith and Paul (1990) reported average microbial biomass pool size for grassland systems of 1090 kg C / ha.

Univariate statistics also indicated how soil properties varied with distance from the *A. tridentata* axis (i.e., center of the plot; Figs. 3A–C). Concentrations of H_2O-C and SIR-C were greatest within 25 cm of the plant axis and lowest at distances beyond 60 cm (Figs. 3B, C). A similar pattern was observed for TI-N except that mean concentration was low in soil collected from directly beneath the *A. tridentata* plant (Fig. 3A) and from distances beyond 60 cm. This somewhat unexpected finding of a resource "hole" in the center of the resource island may be indicative of differences in the cycling of N under sagebrush and grass plants.

Variography indicated that samples of TI-N, H_2O-C, and SIR-C were spatially correlated (Fig. 4). Correlograms for SIR-C and TI-N exhibited similar ranges of about 0.7 or 0.8 m. The correlogram for H_2O-C was similar to the others at small lag distances and equaled the sample variance at a range near 0.7 m. However, at greater lags, correlogram values for H_2O-C increased above the sample variance and did not appear to reach a sill until lags were greater than 1 m. A correlogram sill greater than 1 for H_2O-C can occur if the majority of sample values are collected from an area with dimensions equal to or less than the variogram range (Barnes 1991) or if discrete regions of high and low concentration occur at lags greater than the maximum lag in

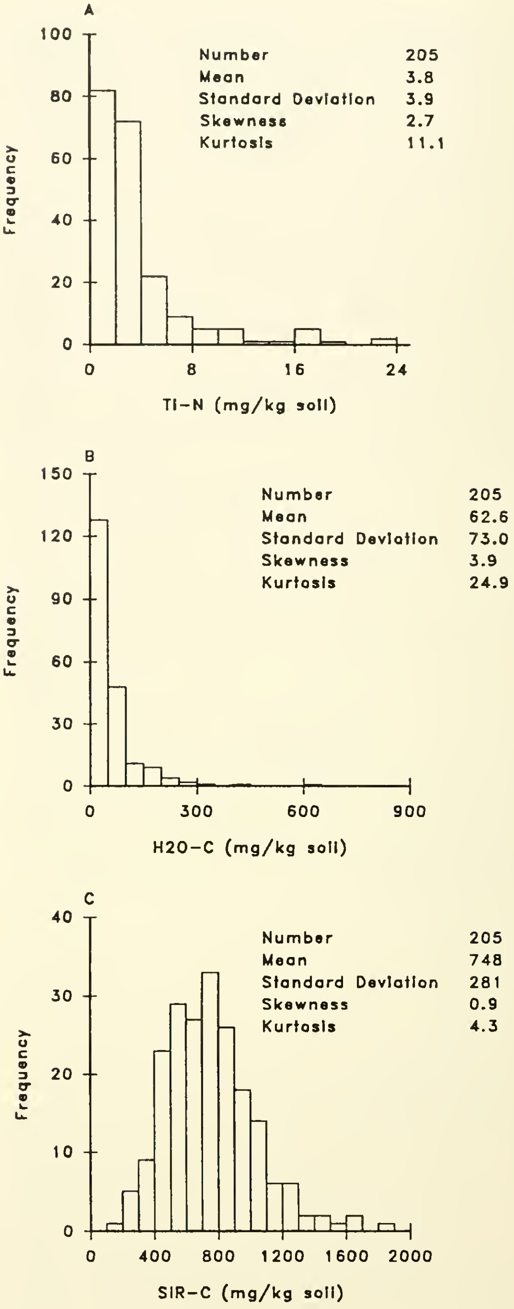

Fig. 2. Frequency histograms and some basic summary statistics for (A) total inorganic-N (TI-N), (B) water soluble-C (H_2O-C), and (C) soil microbial biomass-C (SIR-C).

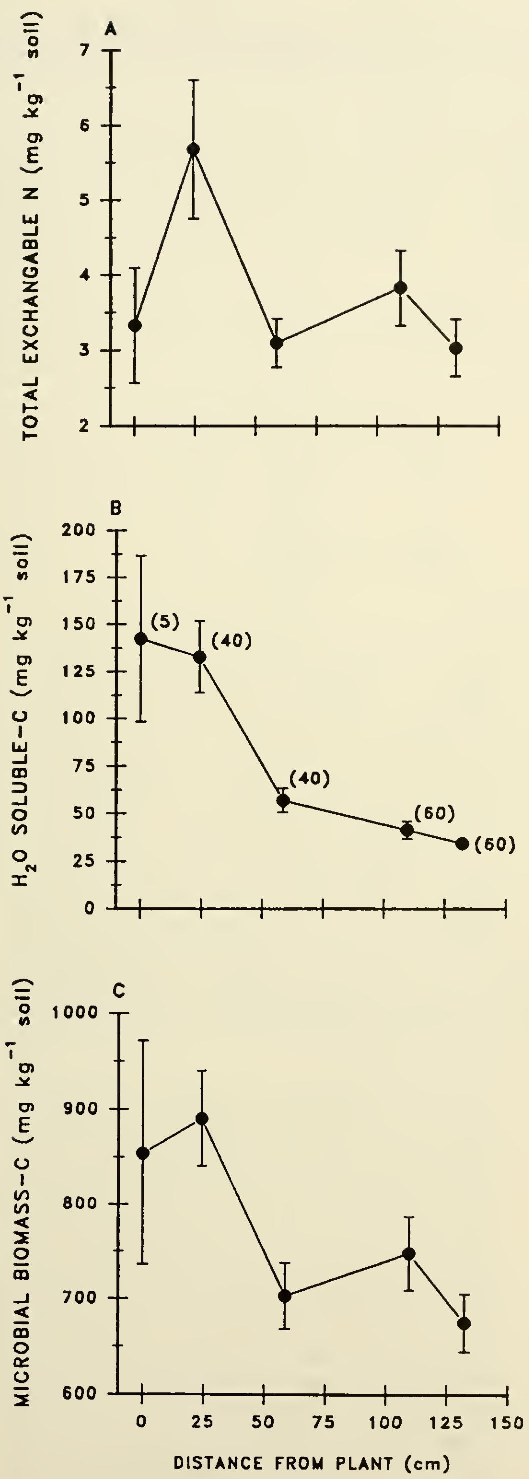

Fig. 3. Mean ± standard error for (A) TI-N, (B) H_2O-C, and (C) SIR-C. Numbers in parentheses are the number of data points (from five plots combined) that contribute to each estimate.

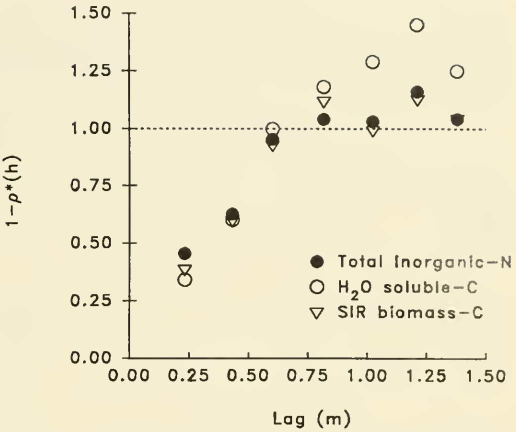

Fig. 4. Omnidirectional correlograms for TI-N, H_2O-C, and SIR-C. Each point shown was calculated from a minimum of 253 pairs (range 253–644).

the correlogram (i.e., an incompletely modeled "hole" effect). The apparent nuggets for all three soil parameters suggested that more than 75% (a correlogram value of 0.25 or less) of total sample variability could be modeled as spatial dependence.

Ranges observed in correlograms of soil properties were used to establish the separation distance beyond which correlation between samples could not be distinguished from sample variance. In other words, samples separated by distances greater than the range were candidates for analysis using more traditional statistical techniques that assume independence such as ANOVA. For our data, samples in the first two distance classes were thus combined and compared to samples from the last two classes because they were separated by more than about 0.8 m. Samples in the third distance class, lying at an intermediate distance between the center and outer boundary of the plot, were excluded from analysis. Analysis of variance of $\log_{10}$ transformed data using the five plots as blocking factors showed mean concentrations of TI-N, H_2O-C, and SIR-C to be significantly greater ($P < .001$) within 29 cm of the plant axis than values collected ≥ 1.07 m away from the plant axis (Table 1).

Omnidirectional correlograms characterized spatial correlation or continuity purely as a function of lag distance. However, by considering the orientation of samples in addition to their lag distance, directional anisotropies were suggested. Directional correlograms showed

TABLE 1. Summary statistics and randomized complete block ANOVAs for $\log_{10}$ transformed TI-N, H_2O-C, and SIR-C. Data are summarized into two sample location classes: **Near** (all measurements collected from within 29 cm of the plant axis; $n = 45$) and Away (samples collected at distances greater than 107 cm from the plant axis; $n = 120$). Average separation distance between the two location classes was 99.4 cm.

	Mean		Standard deviation		Standard error	
	Near	Away	Near	Away	Near	Away
TI-N	0.58	0.39	0.34	0.32	0.05	0.03
H_2O-C	2.01	1.49	0.31	0.26	0.05	0.02
SIR-C	2.93	2.82	0.14	0.17	0.02	0.02

Source of variation		df	MS	F	P
	Plot	4	0.59	6.14	<.001
TI-N	Sample Location	1	1.14	11.81	.001
	Error	159	0.10		
	Plot	4	0.21	2.85	.026
H_2O-C	Sample Location	1	8.79	122.49	<.001
	Error	159	0.07		
	Plot	4	0.06	2.32	.060
SIR-C	Sample Location	1	0.36	13.63	<.001
	Error	159	0.03		

differences in both nuggets and ranges (Fig. 5). Generally, the largest apparent nuggets were observed in correlograms oriented in the 0° (east-west) and 45° (northeast-southwest) directions. With the exception of H_2O-C, these correlograms had estimated nuggets of 0.4 or more. Conversely, correlograms calculated for the 90^0 (north-south) and 135^0 (northwest-southeast) directions generally exhibited nuggets of ≤ 0.2.

Directions of maximum and minimum continuity were identified. For TI-N, maximum continuity was observed in the 45° direction while lower but similar ranges of continuity were observed in the other three directional correlograms (Fig. 5, left column). Little anisotropy was observed in directional correlograms for H_2O-C, suggesting that spatial correlation could be adequately modeled with a single isotropic correlogram (Fig. 5, center column). Like TI-N, the direction of maximum continuity observed for SIR-C was 45°, with a direction of minimum continuity in the 135° direction (Fig. 5, right column). The anisotropies for TI-N and SIR-C were accounted for in kriging by using a model that evaluated both distance and direction (Table 2).

Maps of the estimates generated with these models and ordinary kriging were constructed for each soil property in each plot. Taken together they suggest that generalizations about spatial distribution of resources in the soil beneath *A. tridentata* can be complicated by the variation observed between individual plants and specific soil properties. For example, distinct "islands" of TI-N were not always clearly associated with *A. tridentata*. Instead, in three of five plots highest concentrations of TI-N appeared to be associated with location of grasses (Fig. 6, plots A,B,E). In plots C and D, concentrations of TI-N were highest in the vicinity of the *A. tridentata* canopy. However, vegetation maps of these plots indicate that grass species were present near the *A. tridentata* plant. In plot E smallest concentrations of TI-N were predicted to lie under the *A. tridentata* plant.

Conversely, highest accumulations of H_2O-C were clearly associated with *A. tridentata* in kriged maps. In each plot high concentrations of H_2O-C were localized near the plot center under the plant canopy. Location of grass species did not always appear to coincide strongly with high concentrations of H_2O-C (see NW 1/4 of plot A, NE and SE 1/4 of plot B, and NE 1/4 of plot E). However, high concentrations of both TI-N, and H_2O-C did coincide with location of grasses in the NW 1/4 of plot B and SW 1/4 of plot E.

Maps of SIR-C indicate that islands of soil biomass-C were present under plants but not apparently specific to any particular type of vegetation. Relatively high concentrations of SIR-C were estimated under *A. tridentata* plants in all plots. However, SIR-C was also

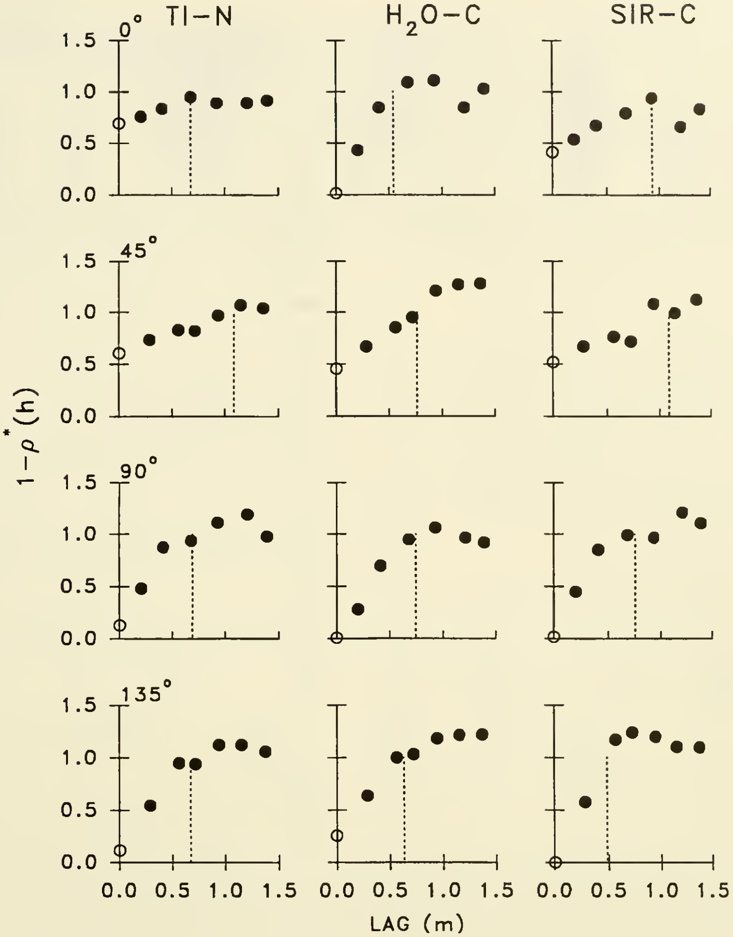

Fig. 5. Directional correlograms for TI-N, H_2O-C, and SIR-C in the 0°, 45°, 90°, and 135° directions calculated with a tolerance of ±15°. Each point shown was calculated from a minimum of 47 pairs (range 47–212). Vertical lines correspond to a correlogram value of 1 and were used to identify directions of maximum and minimum spatial continuity. Open symbols are estimates of the apparent nugget (the apparent ordinate) fit by eye.

accumulated elsewhere in relation to the location of grass species. High concentrations of SIR-C were observed in several instances not associated with high concentrations of either TI-N or H_2O-C (e.g., NE and SW 1/4 of plot B, NW 1/4 of plot D).

Cross-variography indicated how TI-N, H_2O-C, and SIR-C covaried spatially with respect to *A. tridentata* and grass species. Indicator transformed TI-N data were similarly and positively correlated with *A. tridentata* and grass species at a lag of 0 (equivalent to the Pearson correlation coefficient; Figs. 7A,B). However, correlation varied with increasing lag distance (i.e., showed spatial dependence) in a different manner for each. For *A. tridentata* highest positive correlations with TI-N were observed in the 45° (northeast) and 90° (north) directions (Fig. 7A). The range over which *A. tridentata* remained positively correlated with TI-N was longest in the 45° and 90° directions, extending to about 1 m and 0.75 m, respectively. Positive correlations with TI-N were observed for other directions too but only to a lag of about 0.5 m. In contrast, grass species were positively correlated to above-median TI-N concentrations in the 315° (southeast), 270° (south), and 225° (southwest) directions (Fig. 7B). The range over which grass species were positively correlated to TI-N in these directions was less than that for *A. tridentata*. In other directions grass species were uncorrelated or negatively correlated to TI-N at lags above 0.

TABLE 2. Model[1,2] parameters used for ordinary kriging ALE soil properties.

Soil parameter
TI-N
$1\text{-}\rho^*_{45} = .154 + 0.428\ \mathrm{Sph}(0.27) + 0.524\ \mathrm{Sph}(1.80)$
$1\text{-}\rho^*_{135} = .154 + 0.428\ \mathrm{Sph}(0.71) + 0.524\ \mathrm{Sph}(1.20)$
SIR-C
$1\text{-}\rho^*_{45} = .072 + 0.381\ \mathrm{Sph}(0.23) + 0.717\ \mathrm{Sph}(1.87)$
$1\text{-}\rho^*_{135} = .072 + 0.381\ \mathrm{Sph}(0.74) + 0.717\ \mathrm{Sph}(0.75)$
H_2O-C
$1\text{-}\rho^* = 1.40\ \mathrm{Sph}(1.3)$

[1] Models shown for TI-N and SIR-C are a combination of a nugget constant and two spherical models. The spherical model, denoted "Sph," is an authorized model commonly used to model variograms. The number that precedes "Sph" can be thought of as the local sill for that model while the number in parentheses is the range at which the local sill is reached (see Isaaks and Srivastava 1989). For a correlogram, the standardized form is $1\text{-}\rho^*(h) = 1.5\,(\text{lag/range}) - 0.5\,(\text{lag/range})^3$ if lag ≤ = range, else 1 if otherwise.

[2] NOTE: Geostatisticians often distinguish between the nugget used for diagnostic purposes, which is the *apparent* ordinate intercept, and the nugget value, which is used in modeling.

Indicator transformed H_2O-C data were positively correlated with *A. tridentata* but not with grass species at a lag of 0 (Figs. 7C,D). As with TI-N, highest correlations with *A. tridentata* were observed in the 45° and 90° directions (Fig. 7C). Similar patterns of spatial dependence were observed for all directions. The distance to which H_2O-C remained positively correlated with *A. tridentata* ranged from a minimum of about 0.5 m to a maximum of near 0.75 m in the 45° and 90° directions. Unlike *A. tridentata*, H_2O-C was not positively correlated with grass species (Fig. 7D). Instead, H_2O-C was moderately negatively correlated in the 0°, 45°, 90°, and 135° directions, meaning grass species were more associated with below-median concentrations of H_2O-C. At lags greater than about 0.2 m, little change in cross-correlograms was observed, indicating only a weak spatial dependence.

In contrast to H_2O-C, cross-correlograms indicated that SIR-C was slightly more correlated with grass species than with *A. tridentata* at a lag of 0 (Figs. 7E,F). Like other soil properties, strongest positive correlation between *A. tridentata* and SIR-C was observed in the 45° direction, which also remained positively correlated to lags in excess of 1 m (Fig. 7E). Lowest correlations with *A. tridentata* were to the 270° and 225° directions. Indicator transformed SIR-C data were most correlated to grass species in the 225°, 270°, and 315° directions (Fig. 7F). Spatial dependence of correlations was observed out to a lag of about 0.5 m. Beyond this, correlations of grass species with SIR-C remained approximately constant.

DISCUSSION

Geostatistics can be applied to resource island data to provide several useful diagnostic features prior to actual mapping of the landscape itself. For example, variography can define the presence and extent of spatial correlation and alert the researcher to apply with caution classical statistical comparisons that assume samples are independent and from identically distributed populations. For these methods to be more properly applied to spatial data, comparisons should probably be limited to those samples separated by distances ≥ range of the correlogram (Table 1; Webster 1985, Robertson 1987). This is true for studies that compare samples collected along a continuum such as distance, depth, or concentration (i.e., resource gradient) or as a function of time.

Another promising use of variography is to relate spatial continuity of two or more variables at the same site or the same variable at two or more sites by comparing variograms, covariograms, or correlograms with one another. This approach may be useful for comparing the scale of ecological processes or ecosystem boundaries, but should be approached with caution for several reasons. First, each point in a traditional variogram represents the *average* value of the squared difference between many pairs of data points. While an average value may be appropriate for modeling spatial continuity (as a summary statistic), it does not indicate the range of individual squared differences or provide an estimate of the "goodness of fit" about each point in a variogram. The range of the deviation about the average value may be large or small (see Webster and Oliver 1992), complicating comparisons of variograms. Thus, for comparative purposes other more "robust" representations of spatial dependence such as Journel's mAD estimator, Cressie-Hawkins' robust estimator, or the rodogram (see Rossi et al. 1992) may be more appropriate choices. Second, even if variograms for two properties are similar, resultant estimates may yield very different maps (e.g., TI-N and SIR-C in this study). This is because estimation of unknown data values by kriging depends not only

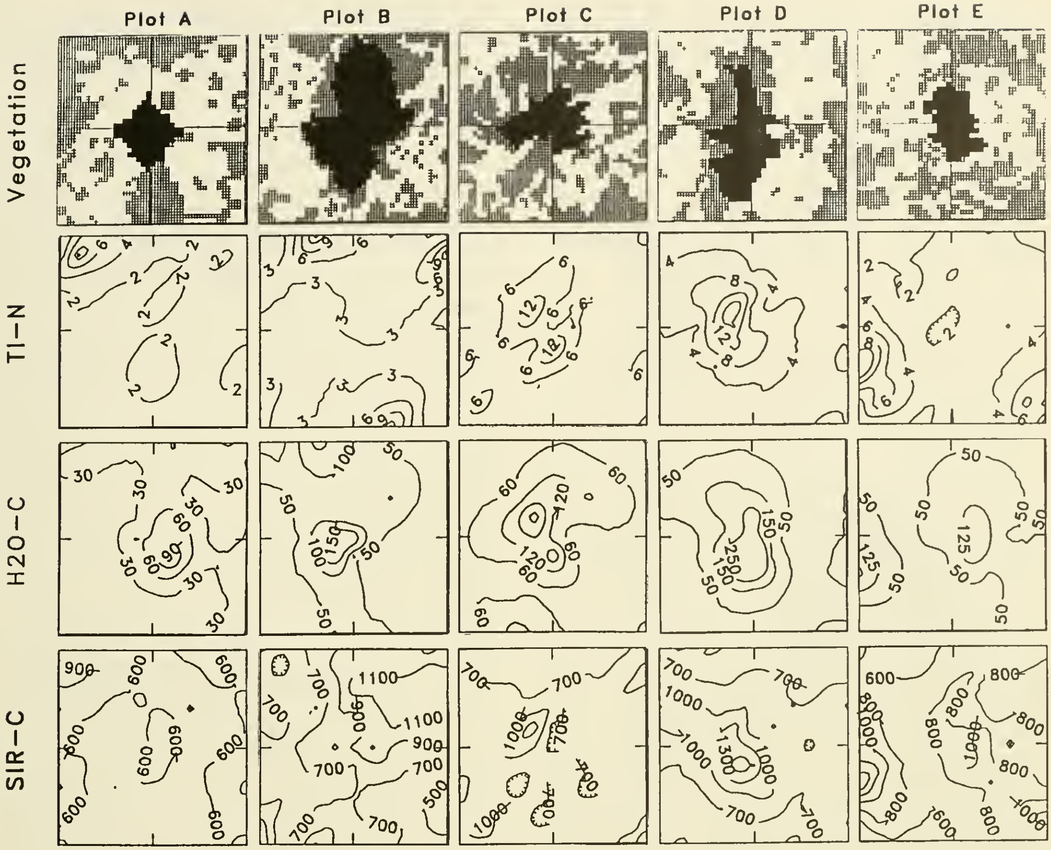

Fig. 6. 2 × 2-m maps of vegetation and kriged estimates of TI-N, H_2O-C, and SIR-C for five ALE plots. Each kriged plot is composed of 1681 points estimated by ordinary point kriging. Vegetation maps indicate vertical projections of *A. tridentata* (black) and grass species (crosshatch) as determined from photographs. Soil properties are depicted in mg / kg soil (dw).

upon a model of spatial continuity, but ultimately upon degree and configuration of the known sample values in the field.

During our analysis of resource island data using geostatistical methods, we made several assumptions or decisions about the data that could have affected our interpretations. First, we assumed that resource islands under *A. tridentata* could be monitored using a particular configuration of samples located within a 2 × 2-m plot. A different number of samples collected from a larger plot with a different shape or in a different pattern might have generated different correlogram models or kriged estimates (Webster and Oliver 1992). Second, we collected data at a single time during the year, thereby making the kriged maps "snapshots" in time and space. Data values and spatial continuity undoubtedly vary for some types of environmental variables (e.g., soil moisture or TI-N) on a seasonal or shorter time scale. Other environmental variables such as soil texture, total-N, or C might change more slowly. Third, we chose to analyze data for the five plots collectively rather than for each plot individually. This choice reflects an interpretation that correlograms for individual plots were reasonably similar to each other and allowed our calculations to be based on a greater number of paired comparisons. We reasoned that correlogram models of spatial continuity, derived from concatenated data, would *summarize* typical patterns of spatial continuity and directional anisotropies. Alternatively, although single-plot analyses would result in plot-specific models of spatial continuity with greater specificity, they might make generalizations difficult. Finally, we assumed that spatial continuity for H_2O-C was reasonably described by a single isotropic model, but we concluded

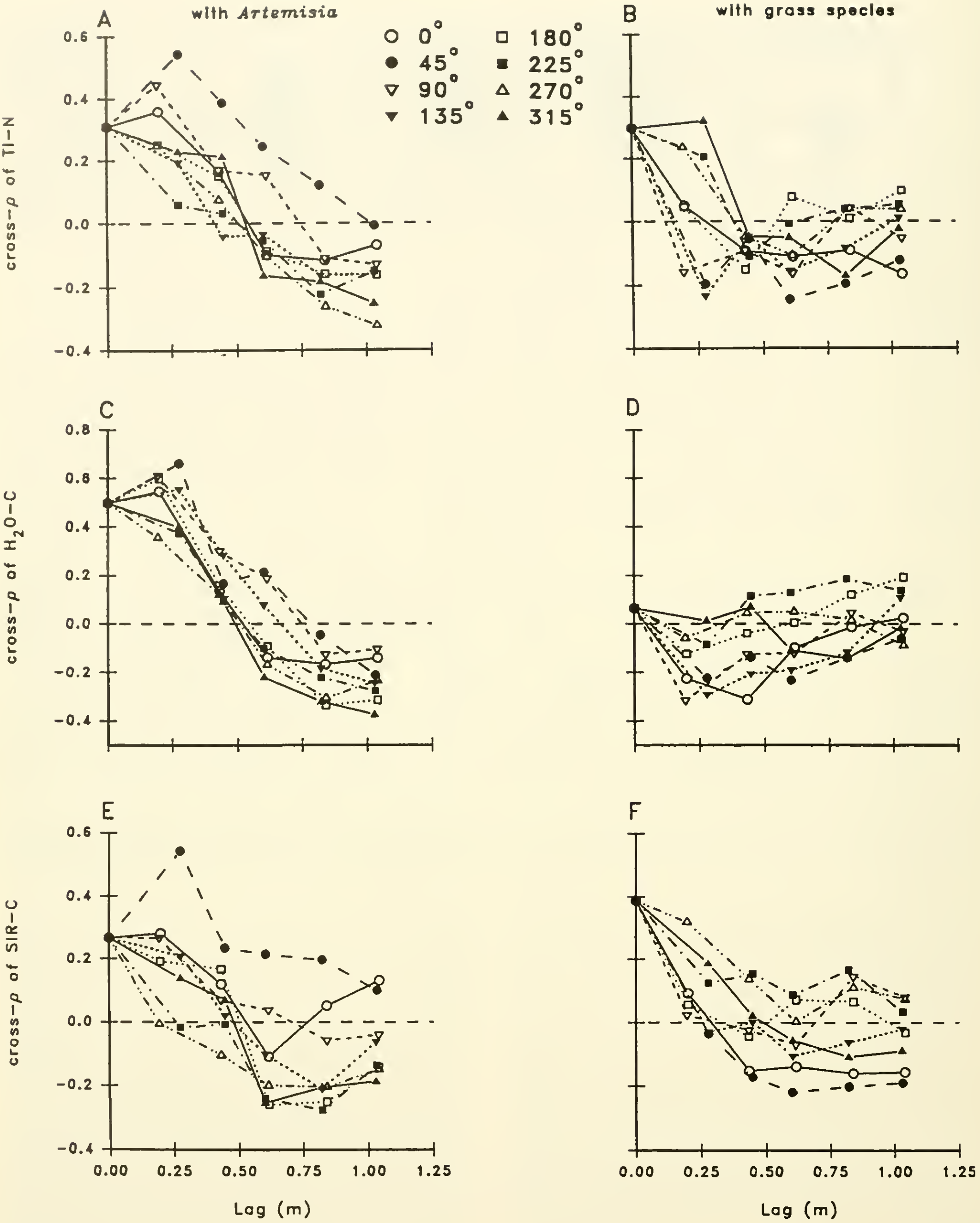

Fig. 7. Directional cross-correlograms showing spatial covariance of indicator transformed TI-N, H_2O-C, SIR-C data, and presence/absence (coded as 1 or 0) of *A. tridentata* and grass species. Correlograms were calculated for 0° (east), 45° (northeast), 90° (north), 135° (northwest), 180° (west), 225° (southwest), 270° (south), and 315° (southeast) directions ±30° tolerance. Each point shown summarizes a minimum of 54 pairs (range 54–158).

that directional anisotropies observed for TI-N and SIR-C were important enough to be accounted for in the estimation process.

Results of a geostatistical analysis cannot completely replace "sound ecological reasoning" or theory (Rossi et al. 1992). Thus, the researcher must decide whether directional anisotropies observed in descriptive variography portray significant spatial patterns or are merely a coincidental result of the number and arrangement of data. The decision to account for spatial anisotropy in the kriging procedure is, in part, related to the desired end product of the geostatistical analysis. For example, if the goal of an analysis is the most accurate representation possible of a particular resource island under a specific *A. tridentata*, then a highly detailed model of spatial continuity would be appropriate regardless of the source of spatial variability. In this case variography based on a concatenated data set might be less appropriate than analysis based only on the single plot. However, the goal of geostatistical interpretation of ecological data may not be to produce detailed site maps. Instead, the ecologist may be more interested in patterns that are broadly applicable. Anisotropies can often be related to information about the environment such as stratigraphic, meteorological, or hydrogeological patterns (Isaaks and Srivastava 1989) and may suggest linkages between environmental variables. Our decision to account for anisotropies in the kriging process was, in part, influenced by information about another environmental parameter, prevailing wind direction. For this reason we would expect the anisotropies observed for TI-N and SIR-C to be a consistent feature of the ALE landscape.

Directional correlograms revealed greatest spatial continuity for samples of TI-N and SIR-C in the 45° direction, northeast-southwest. Cross-correlograms, more specifically, indicated that above-median concentrations of soil properties were most correlated to *A. tridentata* in the 45° direction, or northeast. For the ALE site, cumulative records indicate that prevailing local wind direction is from the southwest quadrant (Table 3), corresponding to the downwind direction of greatest spatial continuity. Prevailing wind direction might influence spatial patterns of soil resources by affecting distribution of litter deposition which, for *A. tridentata* at the ALE site, may exceed 60 kg / ha annually (Mack 1971).

TABLE 3. Frequency of occurrence of wind at the ALE site. Source: H. Bolton, Pacific Northwest Laboratory.

Source quadrant	1990		1991	
	Hours	Percent	Hours	Percent
0–90° (NE)	1161	13.25	1208	13.97
90–180° (SE)	1557	17.78	1613	18.66
180–270° (SW)	4090	46.70	3974	45.96
270–360° (NW)	2227	22.27	1851	21.41

Evidence for the occurrence of resource islands in the ALE landscape was provided by comparing concentrations of soil resources collected near *A. tridentata* vegetation to those collected away from the plant. However, the specific sampling regime employed to evaluate "near" vs. "away" influenced the particular conclusion reached. For example, Bolton et al. (1990) were unable to conclude that concentrations of TI-N in soil under *A. tridentata* were significantly greater than concentrations measured in open soil crust based on six samples drawn at random from each soil type (see also Doescher et al. 1984). In contrast, we found that evaluating TI-N vs. distance away from the *A. tridentata* axis resulted in the naive conclusion that significantly higher concentrations of TI-N would always occur under *A. tridentata* plants (Fig. 3A, Table 1). Such a conclusion for TI-N and other soil properties would lead to a model of a landscape composed of identically sized, symmetrical resource islands centered on each *A. tridentata* individual and would infer some sort of causal relationship between concentration of TI-N and *A. tridentata* presence. However, kriged maps suggest that greatest concentrations of TI-N were not always associated with *A. tridentata*.

Autocorrelation of soil properties was described using variography. The association of soil variables with *A. tridentata* individuals was supported jointly by kriged maps and cross-correlograms, with the latter showing that soil properties (especially H_2O-C) were positively correlated to *A. tridentata*. Kriging is a means for producing visually satisfying maps of soil properties and provided additional insight into characteristics of resource distribution under *A. tridentata*. However, we relied on these maps primarily as heuristic tools because we recognized that kriged maps are models that can be influenced by decisions about the data set (e.g., concatenated vs. single plot), the "art" of variogram modeling, the type of kriging chosen (ordinary kriging is a data "smoother"), the specific search strategy used, and the method of graphical representation. Finally, kriging by itself does not provide a measure of estimate confidence or reliability like nonparametric methods (Journel 1983) or stochastic conditional simulation (Rossi et al. 1993).

Kriged maps of H_2O-C appeared to be most similar to graphs of summary statistics vs. distance from plant axis (Fig. 3A). In each kriged map (Fig. 6), high concentrations coincided with *A. tridentata* in a classic resource island pattern. These accumulations might be tied closely to inputs from *A. tridentata* litter fall representing a source of C that could be accessed by heterotrophic soil microorganisms. Alternatively, high concentrations of H_2O-C under *A. tridentata* might not indicate large C inputs. Instead, they might indicate the accretion of soluble, but recalcitrant, forms of C not readily useable by soil microorganisms. In this case the term "resource island" would be ambiguous. To have ecological significance, a resource island must be evaluated for resource quantity, resource quality, and presence of alternative resource substitutes. Further, the significance of resource accumulation into islands might change with time in relation to diurnal cycles, growing season, or successional stage (Halvorson et al. 1991).

Kriged maps of SIR-C showed accumulations of soil microbial biomass in close proximity to each *A. tridentata* individual. However, high concentrations were also observed for locations corresponding to other plant species, demonstrating that resource islands of microbial populations or activity can be numerous and are nonspecific to *A. tridentata*. Additionally, a significant amount of SIR-C was estimated for locations not associated with any plant. This suggests that while local inputs by plants may stimulate microbial population growth or activity, sufficient resources exist in the environment to support moderate amounts of SIR-C during some times of the year. However, plant location may control the distribution of SIR-C indirectly through influence on microclimatological factors such as soil temperature and evapotranspiration. These factors would become more important during the hot, dry summer months and could limit distribution of SIR-C to locales closer to *A. tridentata*.

Assessing the distribution of soil microbial populations or microbially mediated nutrient-cycling processes such as mineralization or denitrification is complicated by multiple resource requirements and compensatory capabilities of living microorganisms (Smith et al. 1985). For example, microbial population size or activity within a C-substrate resource island might be limited by the availability of soil N. Conversely, the same microbial population might be limited by the availability of C-substrate despite an N-rich environment. Under such a scenario the greatest population size or activity might occur in a location with low or intermediate quantities of both C and N, and the resource island for soil microorganisms or mineralization potential would appear distinct spatially from other resources. Estimation of soil properties like SIR-C that depend on the distribution of one or more other resources may need to be evaluated with respect to temporal and spatial distributions of alternative resources.

Kriged maps of various soil properties can be interpreted within the context of the relationship between the particular soil parameter and *A. tridentata*. Our data indicate that shape and orientation of resource islands under *A. tridentata* vary with the specific soil property considered, need not be centered on the axis of an *A. tridentata* plant, and need not be symmetrical. The maps also provide evidence that suggests a vertical projection of the plant canopy is not well correlated to the distribution of soil variables and thus should not be used as a basis for sampling designs (Fig. 6). For some soil properties (e.g., H_2O-C) the difference between values characterizing the resource island and those characterizing the surrounding matrix may be large and the resource island may appear to have sharp boundaries. Conversely, the range of data values for other soil properties (e.g., SIR-C) may be smaller and the transition from resource island to the surrounding soil matrix more complicated. Resource island boundaries may also change with direction, making sampling designs based on only a few transects questionable. Finally, resource islands do not occur under all *A. tridentata* or for all soil properties.

Other plants like annual and perennial grasses can be the focal points for resource islands of some variables (Jackson and Caldwell 1993b).

Geostatistics allows estimation and mapping of resource islands in considerable detail. Such maps can be used to further our understanding of the ecology of *A. tridentata,* refine nutrient budgets for shrub-steppe ecosystems, reveal the existence of resource and process-dependent patterns, and help provide a rationale for sampling designs based on natural boundaries. Besides two-dimensional space, geostatistics can be used to consider differences in spatial continuity with soil depth (i.e., a third dimension) or time (via repeated measurements). However, even with geostatistics, our definition of a resource island can be improved. Whether a resource island is more properly delineated by some minimum difference in resource concentration or related to the ecological significance of small differences in concentration remains to be answered. Further, the resource island "effect" may be related to more than a single environmental parameter. Consequently, methods must be developed to simultaneously integrate information for several environmental variables and summarize them spatially.

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HABITAT PREFERENCE AND DIURNAL USE AMONG GREATER SANDHILL CRANES

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ABSTRACT.—We examined patterns of habitat use by Greater Sandhill Cranes (*Grus canadensis tabida*) in the Intermountain West, April–October 1991–92, to determine whether cranes exhibited a specific preference for crops, fields, and areas within a field. This information will help farmers and wildlife managers direct nonlethal control methods to the sites where crane damage is most likely to occur. We conducted surveys along two 37-km transects weekly in Cache Valley, Utah, and biweekly in Bear River Valley, Rich County, Utah, and Lincoln County, Wyoming. We recorded 5814 cranes in 662 separate groups. Most were located in pasture/hay (34%), small grain (39%), alfalfa (9%), plowed (9%), fallow (4%), or corn (1%) fields. An index of feeding activity for each field and habitat type suggested cranes fed at approximately the same rate in each field and habitat type. Crane diurnal activity patterns during summer and fall revealed that grainfields were used heavily throughout the day.

Key words: Greater Sandhill Cranes, Grus canadensis tabida, *habitat, depredation, diurnal activity, Utah, Wyoming.*

The most recent population estimate for the Rocky Mountain Greater Sandhill Crane is 17,000–20,000 (Drewien et al. 1987:27). Records of local summer populations are less complete, but the crane population in Cache Valley, Utah, has increased from 14 individuals in 1970 (Drewien and Bizeau 1974) to approximately 200 in 1990 (Bridgerland Audubon Society 1990). Between 1985 and 1987, Rowland et al. (1992) reported 255 cranes summering in Lower Bear River Valley, Wyoming.

Crop depredation complaints attributed to cranes are rising concomitantly with population numbers (Lockman et al. 1987). In response to depredation complaints, Wyoming instituted a limited Sandhill Crane hunt in 1982. Utah instituted a hunt in 1989, but the decision generated enough public controversy that the hunt was canceled in 1992.

Cranes are omnivorous (Mullins and Bizeau 1978) and readily feed in agricultural lands, although habitat use seems to vary widely. Agricultural fields comprised 91% of habitat used by wintering cranes in western Texas (Iverson et al. 1985). During spring staging in Nebraska, Krapu et al. (1984) reported that 70% of habitat use was in agricultural lands. Within agricultural fields 99% of use was in corn stubble. Approximately 80% of spring diurnal habitat use in Alaska was in barley (Iverson et al. 1987). In Wyoming crane use of wet meadows and grainfields ranged from 69 to 100% (Rowland et al. 1992).

We examined habitat preferences and foraging habits of summer resident Sandhill Cranes because of increasing depredation complaints from farmers growing corn and small grains (e.g., barley, oats, rye, wheat) in Cache and Rich counties, Utah. As one means of evaluating these problems and potential solutions, we tested the hypothesis that crane use was concentrated in corn and small-grain fields in particular and in agricultural fields in general. High use of a field may alarm a farmer, but little damage may occur if birds are not foraging. Hence, we also tested the hypothesis that cranes forage in habitats in proportion to their availability. In addition, we assessed whether habitat use varied diurnally during summer and fall. Additional questions relevant to selecting an appropriate scale for management include (1) whether cranes use all fields available to them or concentrate their activities in a few fields, and (2) how cranes distribute their activities within fields.

METHODS

The study area is in Cache Valley, Utah, and Bear River Valley, Utah and Wyoming, and includes three contiguous counties: Cache and Rich counties in northern Utah and Lincoln

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County in southwestern Wyoming. A comprehensive description of the area is included in McIvor and Conover (1992). Cranes normally occupy the region from April until early October.

To determine patterns of field use, we established a 37-km transect in Cache Valley and another in Bear River Valley. The transects traversed a sample of habitat types available to cranes, including cultivated fields, pastures, and natural habitats. Sampling was conducted based on a visual survey method similar to that used by Iverson et al. (1985, 1987). Transects were surveyed weekly in Cache Valley and biweekly in Bear River Valley from April through mid-October 1991–92.

Surveys began 2 h after sunrise from a vehicle moving at 40 km/h. Habitats on both sides of the transects were scanned systematically. As cranes were located, a variety of parameters, including type of habitat in use, were recorded. Habitat was categorized by crop (alfalfa, corn, small grain, pasture, hay, or mixed use) or groundcover type (riparian, sage [*Artemisia* spp.] scrub). To examine the distribution of cranes within fields, we recorded the distance between field edge and the individual crane closest to the edge using a range finder. These data produced a distance-to-edge estimate, which we used as a general indication of whether cranes preferentially used edges or interiors of fields. Using the range finder, we also recorded minimum distance from the transect to the crane flock.

Each sighting of cranes was given equal weighting in constructing contingency tables to maintain statistical independence among field-use observations. A few observations of cranes were made in mixed-use fields and on rural roads. These sightings were combined under the miscellaneous category. Early season hayfields were difficult to distinguish from pastures, and these observations were pooled.

Habitat availability was quantified along each transect in July 1991 and 1992. A sample of 125 random points on each transect was selected *a priori*, and each point was located and its habitat type recorded. To be selected as representative of habitat, each point had to meet two criteria. First, any sampling point not visible from the transect was not used. Second, the perpendicular distance from transect to sampled habitat locations was bounded by the distance within which 90% of all cranes had been located during weekly surveys.

An index of feeding activity was developed to allow comparison among habitat types. When ≥ 1 crane was sighted, an individual was chosen at random from the flock and observed for 1 min to determine if the bird was feeding. The result was a logical variable (feed/no feed), and these data were compiled and compared across habitat types.

Quantitative analyses were based on methods devised by Neu et al. (1974). We used a goodness-of-fit test ($P < .05$) to examine the hypothesis that cranes used habitats in proportion to habitat availability, and to determine whether cranes fed preferentially in certain habitat types. We used a Bonferroni Z-statistic to test for habitat and feeding preference. The Z-statistic and resulting family confidence interval for testing each contingency table cell were generated using a Monte Carlo sampling simulation from a binomial distribution, on a mainframe computer using Minitab (1989).

In 1992 we mapped the distribution of grain- and cornfields along the survey transects. We then compared distribution of available fields with the frequency distribution of cranes observed to test the H_0 of equal use among all grain- and cornfields. These data were analyzed using a goodness-of-fit test.

Patterns of diurnal habitat use were recorded over a 5-d period in June 1991 using both transects and during September 1992 using only the Cache Valley transect. Data-collection methods were identical to those used in the habitat-use survey described above, except that transects were sampled 5 times/day: sunrise, 2 h after sunrise, noon, 4 h before sunset, and 2 h before sunset.

We used PC-SAS (SAS Institute, Inc. 1988) and the PROC CATMOD routine to examine June 1991 diurnal-use data, and the PROC FREQ routine to examine September 1992 data. Both SAS routines used a goodness-of-fit test ($P < .05$) to examine the null hypothesis that cranes maintained the same pattern of field use throughout the day.

RESULTS

Fifty-three surveys were conducted in Cache Valley and 29 in Bear River Valley. During two field seasons we recorded 5814 cranes in 662 groups. Most groups were observed in pasture/hay (34%), small grains (39%), alfalfa (9%), plowed fields (9%), fallow (4%), or cornfields (1%). Remaining cranes were located in riparian (3%), sagebrush (1%), and miscellaneous (2%) habitats.

Habitat availability differed between the two survey transects (Table 1). Although the Cache Valley transect contained no sagebrush habitat, the Bear River Valley transect contained extensive sagebrush (61% in 1991, 58% in 1992). Conversely, the Cache Valley transect contained a small amount of corn (7%) in 1991–92, a crop not cultivated in Bear River Valley. Analysis indicated variation in habitat availability between years along each transect, although the change was not statistically significant ($P = .2230$). For these reasons, collapsing the contingency tables across sample sites or across years would have made the results ambiguous.

Cranes were not distributed randomly among nine available habitats in either 1991 ($X^2 = 374.0$, df = 13, $P < .005$) or 1992 ($X^2 = 464.1$, df = 14, $P < .005$). Along the Cache Valley transect, cranes avoided alfalfa and

TABLE 1. Habitat availability, use, and selection among Sandhill Cranes in Cache Valley (C), Utah, and Bear River Valley (B), Utah and Wyoming, in 1991 and 1992.

Habitat	Study area	# crane observations	Expected # crane observations	Proportion of study area (p_{i0})	Proportion observed in each area	95% family confidence interval on (p_i)	Use preference[a]
1991							
Alfalfa	C	6	25	0.130	0.031	$.0 \le p_i \le .067$	–
	B	14	12	0.158	0.182	$.065 \le p_i \le .325$	0
Corn	C	6	13	0.065	0.031	$.0 \le p_i \le .067$	0
	B	0	0	0.0	0.0	nt[b]	nt[b]
Fallow	C	1	4	0.023	0.005	$.0 \le p_i \le .021$	–
	B	0	0	0.0	0.0	nt[b]	nt[b]
Grain	C	60	34	0.174	0.308	$.205 \le p_i \le .405$	+
	B	18	7	0.096	0.234	$.104 \le p_i \le .364$	+
Misc.	C	4	30	0.152	0.021	$.0 \le p_i \le .051$	–
	B	1	3	0.044	0.013	$.0 \le p_i \le .065$	0
Pasture	C	87	70	0.359	0.446	$.346 \le p_i \le .544$	0
	B	35	5	0.070	0.455	$.299 \le p_i \le .610$	+
Plowed	C	22	6	0.033	0.113	$.051 \le p_i \le .174$	+
	B	1	1	0.009	0.013	$.0 \le p_i \le .065$	0
Riparian	C	10	13	0.065	0.051	$.010 \le p_i \le .097$	0
	B	6	1	0.009	0.078	$.013 \le p_i \le .169$	+
Sage	C	0	0	0	0	nt[b]	nt[b]
	B	2	47	0.614	0.026	$.0 \le p_i \le .091$	–
1992							
Alfalfa	C	29	61	0.194	0.092	$.051 \le p_i \le .153$	–
	B	9	9	0.121	0.123	$.027 \le p_i \le .246$	0
Corn	C	2	20	0.0065	0.006	$.0 \le p_i \le .022$	–
	B	0	0	0.0	0.0	nt[b]	nt[b]
Fallow	C	20	24	0.075	0.064	$.025 \le p_i \le .102$	0
	B	3	1	0.010	0.041	$.0 \le p_i \le .123$	0
Grain	C	144	57	0.183	0.459	$.382 \le p_i \le .535$	+
	B	32	4	0.061	0.438	$.274 \le p_i \le .616$	+
Misc.	C	7	34	0.108	0.022	$.003 \le p_i \le .051$	–
	B	0	1	0.020	0.0	nt[b]	nt[b]
Pasture	C	78	84	0.269	0.248	$.172 \le p_i \le .322$	0
	B	25	11	0.152	0.342	$.192 \le p_i \le .507$	+
Plowed	C	28	14	0.043	0.089	$.051 \le p_i \le .134$	+
	B	5	1	0.010	0.068	$.0 \le p_i \le .164$	0
Riparian	C	6	20	0.065	0.019	$.003 \le p_i \le .048$	–
	B	1	4	0.051	0.014	$.0 \le p_i \le .068$	0
Sage	C	0	0	0.0	0.0	nt[b]	nt[b]
	B	2	42	0.576	0.027	$.0 \le p_i \le .096$	–

[a] Habitat use is expressed as selection for (+), use in proportion to availability (0), and avoidance (–).
[b] Not tested; this habitat type was not recorded in the study area.

miscellaneous habitats in both years, selected grain and plowed habitats in excess of their availability, and used pasture in proportion to its availability. Along the Bear River transect, cranes avoided sagebrush habitat, selected grain and pasture habitats, and used alfalfa and plowed habitat types in proportion to their availability. Results from other habitat types along the two transects either varied between years or were not tested due to patterns of sampling or structural zeros in the contingency tables.

We examined distribution of cranes using grain- and cornfields in 1992 and found that certain grainfields received preferential use in Cache Valley (X^2 = 272.4, df = 72, $P < .001$) and in Bear River Valley (X^2 = 42.6, df = 10, $P < .001$). Insufficient data were available for cornfields in 1992. Cranes tended to exploit field interiors but were broadly distributed within fields. In 1991–92 mean distance-to-field-edge for flocks in corn was 82.2 m (n = 7, SE = 21.2) and 72.1 m (n = 250, SE = 7.26) for flocks using grainfields.

Cranes were recorded feeding in 75% of our observations. A goodness-of-fit test was used to examine the distribution of cranes feeding in each habitat type in comparison to habitat availability (Table 2). Feeding cranes were not distributed randomly in 1991 (X^2 = 242.8, df = 13, $P < .0005$) or 1992 (X^2 = 332.4, df = 14, $P < .0005$). Distribution of feeding cranes approximated distribution of all cranes observed, except in the case of riparian habitat along the Bear River transect. While cranes used this habitat type disproportionately to its availability in 1991, they appeared to feed in this habitat type in proportion to its availability. Data for 1992 were insufficient for analysis.

Crane diurnal use of field types varied with time of day (summer diurnal sampling: X^2 = 91.04, df = 48, P = .0002; fall diurnal sampling: X^2 = 72.65, df = 24, $P < .01$). Crane numbers peaked after sunrise, decreased steadily throughout the day, and then increased again before sunset.

DISCUSSION

Crop depredation attributed to cranes was reported by farmers in Cache, Rich, and Lincoln counties (McIvor 1993). Crane damage occurred in spring in the Cache Valley transect, primarily with newly planted corn crops. Cranes pulled up corn plants and consumed the still-attached seed. Farmers also reported minor damage from cranes trampling emergent alfalfa and small grains (winter wheat, barley, oats). The growing season along the Bear River transect in Rich and Lincoln counties is too short for corn production, and crop damage occurred primarily in the fall, affecting small-grain crops (Lockman et al. 1987, McIvor and Conover 1994). Some trampling damage in spring was also reported in this area.

Cranes concentrated activities in small-grain fields during our surveys. Fields planted in corn constituted only 7% of available habitat, and <3% of cranes sighted were in corn. Most activity in cornfields occurred during germination or while plants were young. Thereafter, cranes avoided cornfields until harvest.

Large expanses of sagebrush habitat were little used, although they constituted about 60% of available habitat. Sagebrush habitat may have reduced crane foraging efficiency by creating dense cover, limiting movement, and offering few plant foods. Agricultural fields in Bear River Valley were surrounded by vast expanses of sagebrush, a condition that may have concentrated cranes into agricultural fields.

Feeding activity closely approximated patterns of habitat use, suggesting cranes fed with the same intensity in each habitat type. Migrating cranes in Nebraska relied on a diversity of habitats to provide various components of their diet (Reinecke and Krapu 1986). Alfalfa fields (Walker and Schemnitz 1987) and grasslands (Reinecke and Krapu 1986) provided a source of invertebrates for cranes. Although invertebrates may provide certain proteins absent from plant foods (Reinecke and Krapu 1986), they comprise only a small component of the diet, varying from 3% (Reinecke and Krapu 1986) to 27% (Mullins and Bizeau 1978). In this study cranes appeared to avoid feeding in Cache Valley alfalfa fields, possibly obtaining invertebrates from pastures or plowed fields. In Bear River Valley cranes fed actively in pasture.

Corn (Reinecke and Krapu 1986) and cereal grains (Krapu and Johnson 1990) provide important nutrient sources for fat synthesis in cranes. Habitat use and feeding activity in grainfields, along both transects and in both

TABLE 2. Distribution of Sandhill Cranes observed feeding in various habitat types in Cache Valley (C), Utah, and Bear River Valley (B), Utah and Wyoming, in 1991 and 1992.

Habitat	Study area	# crane observations	Expected # crane observations	Proportion of study area (p_{i0})	Proportion observed in each area	95% family confidence interval on (p_i)	Use preference[a]
1991							
Alfalfa	C	5	17	0.130	0.037	$.0 \le p_i \le .090$	–
	B	11	9	0.158	0.186	$.068 \le p_i \le .356$	0
Corn	C	4	9	0.065	0.030	$.0 \le p_i \le .075$	0
	B	0	0	0.0	0.0	nt[b]	nt[b]
Fallow	C	0	3	0.023	0	nt[b]	nt[b]
	B	0	0	0.0	0.0	nt[b]	nt[b]
Grain	C	44	23	0.174	0.328	$.209 \le p_i \le .440$	+
	B	14	6	0.096	0.237	$.102 \le p_i \le .407$	+
Misc.	C	2	20	0.152	0.015	$.0 \le p_i \le .045$	–
	B	1	3	0.044	0.017	$.0 \le p_i \le .068$	0
Pasture	C	57	48	0.359	0.425	$.313 \le p_i \le .560$	0
	B	27	4	0.070	0.458	$.271 \le p_i \le .644$	+
Plowed	C	18	4	0.033	0.134	$.052 \le p_i \le .239$	+
	B	1	1	0.009	0.017	$.0 \le p_i \le .082$	0
Riparian	C	4	9	0.065	0.030	$.0 \le p_i \le .075$	0
	B	4	1	0.009	0.068	$.0 \le p_i \le .169$	0
Sage	C	0	0	0.0	0.0	nt[b]	nt[b]
	B	1	36	0.614	0.017	$.0 \le p_i \le .085$	–
1992							
Alfalfa	C	20	43	0.194	0.091	$.041 \le p_i \le .155$	–
	B	7	6	0.121	0.149	$.021 \le v \le .319$	0
Corn	C	1	14	0.065	0.005	$.0 \le p_i \le .023$	–
	B	0	0	0.0	0.0	nt[b]	nt[b]
Fallow	C	13	17	0.075	0.059	$.023 \le p_i \le .100$	0
	B	1	1	0.010	0.021	$.0 \le p_i \le .085$	0
Grain	C	106	40	0.183	0.482	$.391 \le p_i \le .577$	+
	B	19	3	0.061	0.404	$.213 \le p_i \le .617$	+
Misc.	C	2	24	0.108	0.009	$.0 \le p_i \le .032$	–
	B	0	1	0.020	0.0	nt[c]	nt[c]
Pasture	C	54	59	0.269	0.245	$.173 \le p_i \le .327$	0
	B	15	7	0.152	0.319	$.170 \le p_i \le .532$	+
Plowed	C	22	9	0.043	0.100	$.050 \le p_i \le .164$	+
	B	4	1	0.010	0.085	$.0 \le p_i \le .234$	0
Riparian	C	2	14	0.065	0.009	$.0 \le p_i \le .032$	–
	B	0	2	0.051	0.0	nt[c]	nt[c]
Sage	C	0	0	0.0	0.0	nt[b]	nt[b]
	B	1	27	0.576	0.021	$.0 \le p_i \le .085$	–

[a] Habitat use is expressed as selection for (+), use in proportion to availability (0), and avoidance (–).

[b] Not tested; this habitat type was not recorded in the study area.

[c] Not tested; insufficient observed frequencies to test hypothesis.

years, were greater than expected. Although midseason grainfields are unlikely to provide dietary components other than invertebrates, cranes probably forage for waste grain in spring stubble and for ripening and waste grain before and after fall harvest.

Certain grainfields, and possibly certain cornfields, are more attractive than others to cranes. Any burden imposed on the agricultural community by crane depredation is not shared evenly by producers. Determining why certain fields are more attractive to cranes and lessening these attractants may help reduce crane problems. Iverson et al. (1987:456) reported that "over 90% of the variation in distribution of staging cranes [in Nebraska] could be explained by the composition and juxtaposition of essential habitat types." Certain fields in our study area may receive chronic use because of their proximity to other habitat types, such as wetlands and roost sites, or because they possess characteristics that enhance predator detection and escape.

It is unlikely that crane presence has a significant negative effect on productivity of pasture, hay, and alfalfa fields. However, the concentration of cranes in small-grain fields, particularly in the fall, poses a potential economic threat to farmers. Delayed harvest of grains in fall due to wet weather is likely to exacerbate the problem because standing grain remains available to an increasing number of prestaging cranes (Lockman et al. 1987).

Diurnal changes in habitat use may allow cranes to forage while minimizing heat stress. Cranes using pasture and hayfields in midafternoon were probably loafing before feeding prior to sunset. For reasons that are unclear, activity patterns observed in Cache Valley were less distinct in Bear River Valley. Cranes may have moved less, visiting fewer habitat types as a result of the pattern of habitat distribution in Bear River Valley. Additionally, the Bear River Valley survey may have included a greater proportion of paired individuals, which remained on territories during early summer (Johnsgard 1991) and subsequently visited fewer habitat types.

Crane depredation occurs under two disparate conditions: in association with spring planting of corn and just before fall harvest of cereal grains. Encouraging rapid germination of corn and early harvest of grains would minimize availability of these resources to cranes during periods of susceptibility to depredation. Crane damage was concentrated in a few fields, rather than being evenly distributed in all fields, indicating that nonlethal techniques to alleviate these problems need to be focused in these same fields. Farmers who experience chronic depredation problems may wish to consider the economic feasibility of producing crops less prone to crane damage.

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SELENIUM GEOCHEMICAL RELATIONSHIPS OF SOME NORTHERN NEVADA SOILS

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ABSTRACT.—Soil samples, one from each of 10 locations in northern Nevada, were evaluated for redox potential, total and extractable selenium, phosphate, free iron oxide, total and ferrous iron. Mole fractions for extractable selenium species were calculated from redox potentials. Data were used to extrapolate general geochemical relationships for soil selenium at the sample sites. Results obtained from one sample per location allowed only the most general conclusions to be drawn. Soil phosphate levels, which affect the adsorption of selenite species on iron oxide by competing for adsorption sites, were not correlated with levels of extractable selenium in this study. This would suggest that selenium would exist in solution, having been displaced from adsorption sites by phosphorus. Ferrous iron, iron oxides, and redox potential had a combined effect on the level of extractable selenium at all sites. Soils in this study support selenite species that are not readily available to plants and therefore could not support vegetation adequate in Se.

Key words: selenium, soil, redox potential, geochemistry, plant bioavailability.

Selenium (Se) is a significant micronutrient in production agriculture; because of this, knowledge of the Se status of rangelands is important. Distribution of total and extractable Se can vary widely over short geographic distances (Fisher et al. 1990). Because the geology of Nevada is complex, relationships between critical plant Se levels and geological formations are difficult to define. Recently, a review of the Se status of soils, plants, and animals in Nevada reported deficiency problems in western Nevada, variable amounts in northern and central portions of the state, and adequate levels in the southern portion of the state. Selenium accumulator plants grow throughout Nevada on limited seleniferous geological formations (Poole et al. 1989; Fig. 1). The narrow gap between essential and toxic concentrations of Se makes it imperative that processes controlling the distribution of this element be understood (McNeal and Balistrieri 1989).

Uptake of Se by plants is governed by many soil and plant factors including type of plant, soil pH, clay content, and mineralogy. Most important factors determining uptake are form and concentration in the soil. Chemical form is controlled by redox potential parameters (pe + pH; Elrashidi et al. 1989, Mikkelsen et al. 1989). Although Se may exist in four oxidation states, selenate (VI) and selenite (IV) are predominant mobile forms in a soil solution and are available for plant uptake.

Redox potentials are important in soils, and theoretical relationships can be used to predict and interpret metal solubilities (Lindsay and Sadiq 1983). Redox potentials have been used in Nevada to interpret observed sequences of minerals in an alteration zone in Ely, Nevada (Raymahashay and Hollard 1969), interpret hydrogeochemistry of the Red Rock, Nevada, area (Fricke 1983), and evaluate trace-element content of sediment and water in west central Nevada (Rowe et al. 1991). Soil redox potential data are lacking for the state.

The purpose of this study was to investigate soil Se geochemical relationships for 10 Nevada sites using redox potential (pe + pH) and extractable and total Se levels. Phosphate (P), iron (Fe), and iron oxide (Fe_2O_3) levels were also investigated to determine their effect on Se bioavailability for plants growing on the soils.

EXPERIMENTAL PROCEDURE

A soil sample was taken from each of 10 sites: Battle Mountain and Gund Ranch in central Nevada (Eureka and Lander counties); Minden (Douglas County); Reno, Red Rock area north of Reno, Spanish Springs (Washoe

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[1] Sierra Environmental Monitoring, Inc., 1135 Financial Blvd., Reno, Nevada 89502.

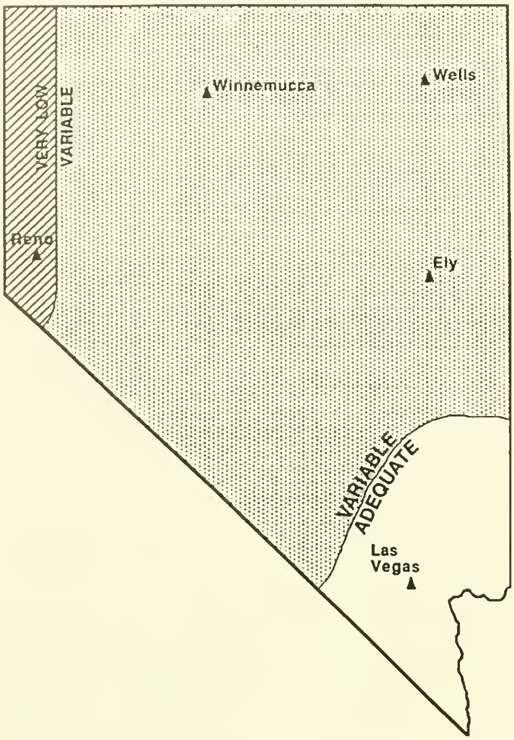

Fig. 1. Selenium in Nevada forage. Very low = 81% of samples with Se concentration of <0.01–0.05 ppm Se; variable = 74% of samples with Se concentration of 0.05–0.5 ppm Se; adequate = 78% of samples with Se concentration of 0.1–1.0 ppm Se.

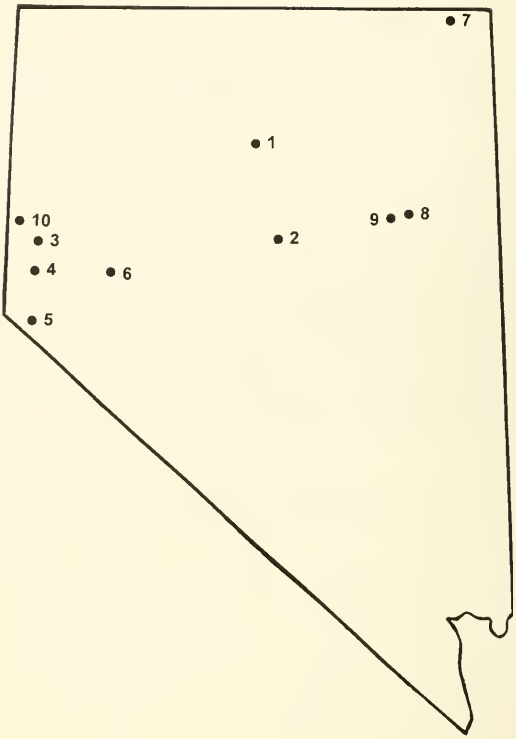

Fig. 2. Soil sample locations in northern Nevada: 1–Battle Mountain, 2–Gund Ranch, 3–Spanish Springs, 4–Reno, 5–Minden, 6–Fallon, 7–Salmon Falls Creek, 8–Huntington Valley, 9–Clover Valley, 10–Red Rock.

County); Fallon (Churchill County); Salmon Falls Creek near Contact and two locations near the Ruby Mountains (Elko County) in Nevada (Fig. 2). Samples were taken approximately 12–15 cm below the surface so as to include the root zone. Air-dried samples <2 mm (No. 10) were used for analysis.

Redox potentials were measured according to the procedure of Lindsay and Sadiq (1983). Soil suspensions were prepared in conical flasks to contain 50 g air-dried soil and 100 mL deionized water. Each treatment was prepared in duplicate, degassed with argon (Ar), stoppered, and shaken. Millivolt readings were taken on soil suspensions with a platinum (Pt) electrode and a glass Ag/AgCl reference electrode using an Altex SelectIon 5000. The platinum/reference electrode system was standardized using a ferrous/ferric ion reference solution (ZoBells; ASTM 1978). Soil suspension pH was determined using a combination electrode that was calibrated with standard buffers (ASTM 1978). Suspension pe was calculated from millivolt readings using the relationship pe = Eh(millivolts)/59.2.

To obtain total soil Se levels, we digested samples in aliquots of 1:1 hydrochloric acid and 5% potassium persulfate for 15 min followed by 3.5% oxalic acid solution for 15 min. The resulting solution was then treated with concentrated hydrochloric acid for 42 min prior to diluting to 100 mL volume with deionized water. Se concentrations of the digests were determined using hydride generation atomic absorption spectroscopy (AAS; Varian SpectrAA 10 with VGA accessory).

Soluble Se was measured in a saturation paste extract from each soil (Jump and Sabey 1989) using hydride generation AAS. The extract Se concentration was used for calculation of Se species. The mole fraction of soluble Se species was calculated employing methods of Elrashidi et al. (1987).

Bicarbonate extractable P was determined using the method of Olsen (Council on Soil Testing and Plant Analysis 1980). To evaluate

Fe_2O_3 levels, we extracted 4 g soil overnight with 4 g sodium dithionite ($Na_2S_2O_4$) and 75 mL deionized water. Suspensions were filtered, brought to volume (Kilmer 1960), and analyzed for Fe by AAS. Total soil Fe was determined by flame AAS on nitric acid digests of soil samples.

Ferrous iron (Fe II) in sample soils was determined colorimetrically. Samples were digested using concentrated sulfuric acid and 30% hydrofluoric acid, neutralized with 4% boric acid, and made to volume with deionized water (Walker and Sherman 1962). To an aliquot of the digest we added 0.001 M bathophenanthroline in 50% ethanol and acetate buffer. Isoamyl alcohol extracted the ferrous-bathophenanthroline complex from the solution. The alcohol layer was drained into a 25-mL volumetric flask, made to volume with 95% ethanol, and the absorption of the solution read on a spectrophotometer (Bausch and Lomb Spectronic 710) at a wavelength of 538 nm. Standards and blanks were treated similarly. Ferrous iron standards were derived from a stock solution of ferrous ammonium sulfate.

For the interpretation of data, we used redox and adsorption relationships developed by Howard (1977), Balistrieri and Chao (1987, 1990), and Schwab and Lindsay (1983) for the behavior of Se, Fe, and PO_4 and equilibria described by Elrashidi et al. (1987) for Se in soils.

Regression and multiple regression analyses were performed following methods of Damon and Harvey (1987). Regressions were evaluated for significance at the 95% confidence level.

TABLE 1. Total selenium, extractable selenium, redox potential (pe + pH), and predominant selenium species in soil samples.

	Selenium*			
Sample location	Total (mg/kg)	Extractable ($\mu g/kg$)	pe + pH	Predominant Species
Battle Mountain[a]	0.62	4	10.0	Selenite
Gund Ranch[b]	0.74	8	11.7	Selenite
Spanish Springs[c]	0.10	102	7.5	Selenite
Reno[c]	0.11	<2	11.1	**
Minden[d]	0.20	50	10.9	Selenite
Fallon[e]	1.2	3	11.1	Selenite
Salmon Creek[f]	0.37	26	8.5	Selenite
Clover[g]	0.13	<2	7.6	**
Huntington[g]	<0.10	<2	9.6	**
Red Rock[h]	0.10	7	11.9	Selenite

*Air-dried basis

**Could not be calculated due to lack of measurable selenium in extract.

[a] Stewart and McKee 1977

[b] USDA-SCS 1978, USDA-SEA 1980

[c] USDA-SCS 1983

[d] USDA-SCS 1984

[e] Willden and Speed 1974

[f] Schrader 1934, Tueller 1975

[g] Tueller 1975

[h] USDA-SCS 1983, Fricke 1983

RESULTS

Total Se, extractable Se, redox parameters, and general site descriptions are presented in Table 1 for sample soils. Mole fractions of the Se species for each sample are presented in Table 2.

Howard (1977) summarized Se geochemistry on an Eh-pH diagram and found that Fe, with which Se is closely associated in both oxidizing and reducing environments, controls Se geochemistry. In aerated soil suspensions the Se (IV) oxyanions $HSeO_3^-$ and SeO_3^{2-} are strongly adsorbed by hydrated surfaces of ferric oxides over the pH range 2–8; above pH = 8, adsorption decreases to complete desorption at pH = 11. Selenite shows a strong affinity for Fe_2O_3 surfaces (Balistrieri and Chao 1987), forming stable ferric oxide-selenite ($Fe_2(OH)_4SeO_3$) complexes that cause immobilization of Se. Selenate on the other hand shows a weaker affinity for oxide surfaces, forming compounds that are soluble and, therefore, mobile (Howard 1977, Elrashidi et al. 1987, Presser and Swain 1990) and easily transportable in groundwater and available for plant uptake (Lakin 1961).

Levels of extractable Fe_2O_3 are presented in Table 3. Because adsorption of selenite increases with increasing concentration of Fe_2O_3 due to the greater number of available binding sites (Balistrieri and Chao 1987), it follows that soils at Gund Ranch and Spanish Springs have the potential to adsorb the largest amounts of selenite. The Clover Valley sample would be least likely to adsorb selenite. pH would not have an effect on the ability of Fe_2O_3 to adsorb selenite for all the soils except Clover Valley (pH > 8). Levels of Fe_2O_3 and Fe(II) had a combined effect on the amount of Se extracted from soils (r = .3196). Iron oxide and Fe(II) were not affected by redox potential (r= .0705).

TABLE 2. Log mole fraction of selenium species[a].

Sample[b]	Species SeO_4	$HSeO_4$	H_2SeO_4	SeO_3	$HSeO_3$	H_2SeO_3	Se^{2-}	HSe	H_2Se
1	–9.2	–14.9	–29.2	–0.15	–0.55	–5.6	–22.9	–15.6	–19.6
2	–5.9	–12.3	–22.6	–0.02	–1.32	–7.0	–33.3	–26.6	–31.1
3	–12.2	–17.9	–24.4	–0.18	–0.48	–7.3	–13.9	–6.3	–10.4
4	–7.4	–12.3	–21.2	–0.55	–0.15	–4.5	–29.9	–21.9	–24.9
5	–6.1	–10.7	–19.1	–0.86	–0.06	–3.9	–35.1	–26.6	–29.9
6	–7.5	–12.9	–22.2	–0.30	–0.30	–5.0	–28.5	–20.8	–25.3
7	–19.9	–19.8	–28.8	–0.59	–0.39	–4.9	–8.39	–0.5	–3.79

[a] Base 10 logarithm

[b] Sample identification: 1–Battle Mountain, 2–Gund Ranch, 3–Salmon Creek, 4–Fallon, 5–Red Rock, 6–Minden, 7–Spanish Springs

Activity of Fe(II) is controlled by $FeCO_3$ (siderite) at pe + pH $\leq$ 8 and by $Fe_3(OH)_8$ (ferrosic hydroxide) at pe + pH $\geq$ 8. In systems below pH = 6.0 with stable redox, less-soluble iron oxides such as geothite (alpha-FeOOH) can control Fe solubility (Schwab and Lindsay 1983). Levels of Fe(II) are presented in Table 3. Ferrous iron levels had a significant effect on the amount of Se extracted from soils (r = .5843). Siderite would control Fe(II) activity in the Spanish Springs and Clover Valley samples. Ferrous iron activity in the remaining samples would be controlled by ferrosic hydroxide. Hematite would control ferric iron activity of sample soils except for Spanish Springs and Clover Valley where ferroselite would control ferric iron (Fe III). Any remaining Fe(III) could be associated with hydrous selenite complexes.

Total Fe levels ranged from 8700 to 28000 mg/kg. Total Se and total Fe were not correlated for these soils (r = –.1028). Redox potential and total Fe had an effect on soil Fe(II) and Fe_2O_3 content (r = .4565 and r = .3998, respectively). A decrease in selenite adsorbed on iron oxide would depend on the adsorption density of selenite (moles of ion adsorbed/kg of oxide; Balistrieri and Chao 1987). Other ions in a soil solution, including P, can compete with selenite for adsorption sites on solid surfaces. Anion adsorption relies on several factors including pH, formation of solution complexes, and competing adsorbates (Mikkelsen et al. 1989). Phosphate displaced all the adsorbed selenite on allophane clays (Rajan and Watkinson 1976) and has been shown to desorb selenate (Singh et al. 1981).

Most P found in alkaline soil exists as calcium phosphate ($CaHPO_4$; Lindsay and Moreno 1960, Boyle and Lindsay 1986). Phosphate levels of study soils ranged from 8.9 to 147 mg/kg P. To evaluate the effect of P on selenite adsorption, we calculated total anion concentration ratios {(anion)/(selenite)}. Results are presented in Table 4. A stronger affinity and larger concentration of one anion should result in more sites being occupied by that anion vs. another (Balistrieri and Chao 1990). Levels of P, and Fe_2O_3 and P did not have an effect on the amount of Se extracted from the study soils (r = .3030 and r = .1019, respectively). Absence of a significant correlation between levels of Fe_2O_3 and P and extractable Se suggests that Se would exist in solution for these soils. Phosphorus would have displaced Se from available binding sites. Selenium-phosphate interactions are generally not of consequence for plant uptake of Se except for plants growing where levels of Se are inadequate to meet animal nutritional needs (Mikkelsen et al. 1989).

Mean concentration of total Se in soils and surficial materials for the western United States is 0.23 mg/kg, with an observed range of <0.10–4.3 mg/kg Se. Most soils from low-Se areas in the United States contain <0.5 mg/kg Se (National Research Council 1983, Boon 1989). A limited survey of Nevada soils, as part of a trace-element survey of soils throughout the United States, revealed a variety of Se levels (Shacklette et al. 1974). Observations in the Fallon area demonstrate that seleniferous spots may be found in alluvial Pliocene deposits occurring over a large part of Nevada, particularly in the Carson and Humboldt sinks (Lakin and Byers 1948, Rowe et al. 1991). Total soil Se levels in this study ranged from <0.10 to 0.74 mg/kg. As with many other elements, total concentration of Se in soils shows little relationship to Se concentration in plants grown in those soils.

TABLE 3. Total iron, extractable iron oxides, and ferrous iron in soil samples.

Sample location	Milligrams/kilogram[a]		
	Total Fe	Oxide Fe	Ferrous Fe
Battle Mountain	17000	4575	3290
Gund Ranch	28000	12175	6090
Spanish Springs	19000	8900	7920
Reno	27000	6550	5800
Minden	19000	3950	10940
Fallon	12000	3700	3010
Salmon Creek	12000	2525	8580
Clover Valley	8700	875	7060
Huntington Valley	19000	4350	5300
Red Rock	17000	6350	3220

[a] Air-dried basis

TABLE 4. Extractable phosphate phosphorus, selenite selenium, and phosphate/selenite molar ratios.

Sample location	Phosphate (10E-5 M)	Selenite (10E-7 M)	{(Phosphate)/(selenite)}
Battle Mountain	3.4	1.3	271
Gund Ranch	3.5	2.5	136
Spanish Springs	15.2	28.9	52
Reno	23.9	0	0
Minden	1.4	29.1	5
Fallon	3.4	1.3	269
Salmon Creek	4.3	5.0	85
Clover	5.8	0	0
Huntington	4.6	0	0
Red Rock	4.1	2.5	160

Workmann and Soltanpour (1980) have reported that water-soluble Se is usually <50 μg/kg in normal cultivated soils. Soils in this study had soluble Se levels of <1–102 μg/kg, existing primarily as selenite. The significant correlation between pe + pH and levels of extractable Se ($r = -.4475$) suggests a relationship between the amount of Se available for plant uptake and soil redox potential at the study sites.

Certain native plants of the Great Basin have tendencies to aggregate in relation to temperature gradients, precipitation patterns, physiography, and soils (Tueller 1975, Reveal 1979). Approximately 80% of all forage and grain sampled in western Nevada has been shown to contain <0.10 ppm Se, less than the dietary requirement of 0.10 ppm for grazing animals (Kubota et al. 1967, McDowell et al. 1983, National Research Council 1983). Soil Se concentration can vary widely over a very short geographic distance (Fisher and Munshower 1991). Upper rangeland forage of extreme northeastern Nevada growing on Idavada volcanics and silicic rocks of volcanic origin was found to contain low levels of Se (Carter et al. 1969). In contrast, lower rangelands surrounding a portion of these areas produce forage adequate in Se (Carter et al. 1968). Alfalfa samples taken from the Carson Valley area were found to be below (<0.05 ppm) the dietary requirement of 0.1 ppm Se (Allaway and Hodgson 1964). Forage at Gund Ranch has been shown to contain 0.13–0.17 ppm Se (Poole et al. 1989). Selenium indicator plants are limited to localized areas on seleniferous geological formations in Nevada (Poole et al. 1989) and are not reported to occur within sample site areas.

Forage at the Fallon site would not be expected to contain appreciable amounts of Se. Soil redox potential does not allow for formation of plant-available selenate. In areas adjoining Carson Valley, including Fallon, white muscle disease in sheep has been a recognized problem (Vawter and Records 1947, Kuttler and Marble 1958) for animals raised on native forage. Soil at the Gund Ranch site supports a small fraction of selenate, allowing for growth of forage marginally deficient in Se. Grazing cattle have been found to be borderline deficient in plasma Se at the Gund Ranch site (Poole et al. 1986). Upper rangeland forage in the Salmon Creek area would be deficient in Se because of lack of available soil selenate. Samples lacking measurable amounts of extractable Se would not support growth of Se-bearing forage.

CONCLUSION

Total and extractable Se, redox potential, pH, and P, Fe(II), and Fe_2O_3 levels were different for each of the sample sites. Redox potential and Fe(II) and free Fe_2O_3 levels would affect the quantity of Se available for plant uptake in study soils. Anion concentration ratios indicate that P would influence adsorption of selenite on iron oxide. Soils in this study support selenite species that are not readily available to plants and therefore could not support vegetation adequate in Se.

Soil Se concentration can vary widely over a very short geographic distance. Nevada's complex geology therefore requires evaluation of the Se status of soils and vegetation on a site basis. Further studies are needed to develop a better understanding of the Se status of the state.

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STATUS AND DISTRIBUTION OF THE LARIDAE IN WYOMING THROUGH 1986

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ABSTRACT.—To date, 17 species of Laridae have been reported in Wyoming. Six of these species have known breeding populations in the state: the Ring-billed Gull (*Larus delawarensis*), California Gull (*Larus californicus*), Herring Gull (*Larus argentatus*), Caspian Tern (*Sterna caspia*), Forster's Tern (*Sterna forsteri*), and Black Tern (*Chlidonias niger*). Of these species, the California Gull is the most abundant and widespread. In 1984 approximately 7300 nests existed in Wyoming at six breeding locations consisting of 10 different colonies. In contrast, only small breeding populations have been discovered for the remaining five species. The Herring Gull is the most recent addition among Laridae known to nest in Wyoming. Likewise, two Ring-billed Gull colonies were recently found after not having been documented as breeding in the state for over 50 years.

Although some nesting colonies are threatened by habitat loss and human disturbance, most seem secure at present. Limited nesting and foraging habitat precludes establishment of large breeding populations of most Laridae in the state.

Key words: Laridae, historical records, inventory, population status, distribution, breeding, Wyoming.

Considerable interest and concern exist regarding conservation and management of colonially nesting waterbirds in the United States and elsewhere. These species occupy high trophic levels on aquatic food chains and are sensitive to disturbance of aquatic ecosystems, especially loss of wetland habitat and contamination by chemical pollutants. In addition, because most of these species nest in colonies, they are vulnerable to human intervention.

Findholt (1984) and Findholt and Berner (1988) reported on the status and distribution of the Ciconiiforms in Wyoming. The purpose of this paper is to provide information on the historical and present status and distribution of the Laridae in the state.

METHODS

Data-collection methods utilized were previously reported (Findholt 1984, 1986a, Findholt and Berner 1988). From 1981 through 1986, but more intensively during the 1984–86 period, I conducted a comprehensive statewide inventory for colonially nesting waterbirds in Wyoming. From 4 April to 31 May 1984 and from 28 March to 5 June 1986, I made 15 aerial surveys in fixed-wing aircraft totaling 67.1 h of flight time to locate new nesting areas. Reservoirs, lakes, marshes, and other potential breeding locations not observed during aerial searches were checked from the ground with binoculars or a 20–45X spotting scope. Breeding colonies were usually censused by making total ground counts of nests. Where ground counts were not feasible, I estimated the number of nests (ground estimates). Colonies were censused when most birds were in late incubation or early hatching stages, and censuses were based on a single visit.

As discussed by Buckley and Buckley (1979), a waterbird colony is difficult to define. Therefore, I used Kushlan's (1986) definition, which is an assemblage of nesting birds. Nests were considered active if adult birds were sitting or standing on nests, incubation was observed, or eggs or young were present (McCrimmon 1982).

Additional sources of information included a literature review, an examination of the files of the Wyoming Game and Fish Department, and correspondence with biologists, naturalists, birdwatchers, and others considered knowledgeable of the Laridae in Wyoming. This paper includes records through 31 December 1986.

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RESULTS AND DISCUSSION

Pomarine Jaeger

There is one record of the Pomarine Jaeger (*Stercorarius pomarinus*) from Wyoming. J. and V. Herold observed an adult individual at Burlington Lake (Goldeneye Reservoir), 24 km northwest of Casper, Natrona County, on 15 May 1980. On the following day, O. K. Scott and B. Stratton saw the jaeger at the same location and confirmed its identity.

According to the AOU Check-list of North American Birds (1983), the Pomarine Jaeger breeding range occurs along northern coastal areas in North America. Thus, only accidental occurrence is expected in Wyoming.

Parasitic Jaeger

O. K. Scott discovered the first Parasitic Jaeger (*Stercorarius parasiticus*)in Wyoming at Soda Lake, Casper, Natrona County, on 2 September 1962. Two more Parasitic Jaegers were observed at Jackson Lake, Grand Teton National Park, Teton County, on 22 June 1975 by M. and B. Raynes. On 24 October 1977, H. Downing and M. Collins reported one immature individual at Lake DeSmet, near Buffalo, Johnson County. One year later another immature bird was observed at Lake DeSmet by M. Collins on 28 August. An immature Parasitic Jaeger was seen at Soda Lake, Natrona County, by J. and V. Herold on 14 November 1981. On 4 September 1983, G. Scott found one individual at Bates Creek Reservoir, south of Casper, Natrona County. The most recent record of this species is from Healy Reservoir, east of Buffalo, Johnson County, when H. Downing and M. Collins observed an adult bird on 21 June 1985.

The Parasitic Jaeger is mostly pelagic, breeds north of the conterminous United States, and generally winters offshore along ocean coasts (AOU 1983). Therefore, only accidental occurrence is anticipated in Wyoming.

Franklin's Gull

The first record of the Franklin's Gull (*Larus pipixcan*) in Wyoming is a specimen collected near Wheatland, Platte County, on 6 May 1912 (Grave and Walker 1913). McCreary (1939) stated that this species occasionally occurred in the state, and on 5 May 1933, 37 individuals were seen near Torrington, Goshen County; some birds remained in the area until 12 May. Also, A. B. Mickey observed a Franklin's Gull near Lake Hattie, southwest of Laramie, Albany County, on 7 May 1933 (McCreary 1939). Oakleaf et al. (1982) considered this species a common summer resident and recorded it in 20 (71%) of 28 degree blocks and breeding in one block. The only nesting record is from Beck Lake near Cody, Park County, where U. Kepler found 10–20 nesting Franklin's Gulls in 1977 (Kingery 1977). In my intensive statewide survey for Franklin's Gull nesting sites, I found none at Beck Lake or elsewhere in Wyoming. Based on the lack of suitable nesting habitat at Beck Lake, the validity of this breeding record is questionable.

Breeding records exist for this species in adjacent states of Idaho (Larrison et al. 1967, C. H. Trost personal communication), Montana (Skaar 1980), South Dakota (Johnsgard 1979), and Utah (Behle and Perry 1975).

Bonaparte's Gull

Knight (1902) considered the Bonaparte's Gull (*Larus philadelphia*) a rather rare migrant in Wyoming and provided details of several records from the state. In addition to Knight's records, Grave and Walker (1913) reported one individual taken from near Sheridan, Sheridan County, by Metz. McCreary (1939) indicated that the Bonaparte's Gull was a frequent migrant in eastern Wyoming and sometimes common. This species has been listed as occurring in Yellowstone National Park (Skinner 1925). More recently, Oakleaf et al. (1982) considered the Bonaparte's Gull an uncommon migrant and reported it from 10 (36%) of 28 latilong blocks.

Because this species breeds north of the conterminous United States (AOU 1983) and does not appear to be expanding its range southward, it is highly unlikely that Bonaparte's Gulls will be discovered nesting in Wyoming.

Heermann's Gull

On 26 September 1984, O. K. Scott et al. discovered a Heermann's Gull (*Larus heermanni*) at Soda Lake, approximately 3 km north of Casper, Natrona County (Kingery 1985). This is the first record of this species in Wyoming.

The Heermann's Gull breeds in the vicinity of Baja California and is a coastal species ranging from southern British Columbia south to Guatemala (AOU 1983). Thus, only accidental occurrence is expected in Wyoming.

Mew Gull

Two historical records exist in Wyoming for the Mew Gull (*Larus canus*). One juvenile bird was collected by V. Bailey on Lake Fork, a tributary of the Green River in the Wind River Mountains, Sublette County, on 28 August 1893 (Oberholser 1919). This specimen is located in the U.S. National Museum. Another Mew Gull was taken near Laramie, Albany County, by A. E. Lockwood prior to 1913 (Grave and Walker 1913). No recent records exist for this species in the state.

According to the AOU Check-list of North American Birds (1983), the Mew Gull breeds north of the contiguous United States. Based on the paucity of reports for this species in states that adjoin Wyoming, only accidental occurrence is anticipated in the state.

Ring-billed Gull

In the 1920s the Ring-billed Gull (*Larus delawarensis*) nested on the Laramie plains, Albany County, and on Yellowstone Lake, Yellowstone National Park (Knight 1902, Skinner 1917, Kemsies 1930). It is difficult to assess when the Ring-billed Gull disappeared as a breeding species in these two areas of the state. This species no longer breeds on the Laramie plains (Raper 1975, Findholt personal observation). Also, the Ring-billed Gull no longer nests in Yellowstone National Park (Schaller 1964, Diem and Condon 1967, K. L. Diem personal communication).

Two active Ring-billed Gull colonies were present at two locations in Wyoming during the 1984–86 period. On 21 May 1984, I counted 102 adults of this species and 70 nests with eggs at Soda Lake (42°54′N, 106°18′W), about 3 km north of Casper, Natrona County (Findholt 1986b). Although Ring-billed Gulls continued to nest at Soda Lake in 1985 and 1986, the colony was not censused. One additional Ring-billed Gull nesting colony was found in Wyoming at Ocean Lake (43°07′N, 108°35′W), approximately 24 km northwest of Riverton, Fremont County. On 22 May 1985, I counted 10 adults and 6 nests containing 2–3 eggs each on Peninsula Island. Twenty-three active nests were present on 31 May 1986.

Breeding records exist in adjoining states of Idaho (Larrison et al. 1967, C. H. Trost personal communication), Montana (Skaar 1980), and South Dakota (Johnsgard 1979).

California Gull

Two California Gull (*Larus californicus*) nesting colonies existed historically in Wyoming. One colony was discovered on the Molly Islands, Yellowstone Lake, Yellowstone National Park, in 1898 when Skinner (1917) estimated about 1000 gulls were present. The other colony, which contained an unknown number of California Gulls, was located on an island in Bamforth Lake, about 15 km northwest of Laramie, Albany County, since 1934 (McCreary 1939).

In 1984 there were six breeding locations consisting of 10 different colonies that included approximately 7300 nests (Findholt 1986a). The six sites included both Yellowstone Lake and Bamforth Lake in addition to four recently occupied nesting areas. The new California Gull colonies are located at Pathfinder Reservoir, Carbon County (42°23′N, 106°56′W); Ocean Lake, Fremont County (43°07′N, 108°35′W); Sand Mesa, Fremont County (43°19′N, 108°20′W); and Soda Lake, Natrona County (42°54′N, 106°18′W). Although California Gulls continued to nest at all six locations during the 1985–86 period, none of the colonies were censused. Also, only 5–10 pairs appeared to be present at Sand Mesa in 1985 and none in 1986. The decline in the Sand Mesa nesting population is a result of intentional destruction of nests by the Wyoming Game and Fish Department to supposedly enhance Canada Goose (*Branta canadensis*) production.

The overall increase in the California Gull nesting population in Wyoming since historical times is most likely a result of human-induced environmental changes. These changes have created additional breeding habitat and new food sources (Findholt 1986a).

This species breeds in adjacent states of Colorado (Ryder 1978), Idaho (Larrison et al. 1967, C. H. Trost personal communication), Montana (Skaar 1980), and Utah (Behle and Perry 1975).

Herring Gull

Knight (1902) considered the Herring Gull (*Larus argentatus*) very rare in Wyoming and noted that there was only one record from the state. This species apparently increased in numbers during the early 1900s and was reported as being a common summer resident at Yellowstone Lake and in the Big Horn Basin (Grave and Walker 1913). Later, McCreary

(1939) considered the Herring Gull a moderately common migrant seen around the lakes of the eastern part of the state and along the North Platte River. Recently, Oakleaf et al. (1982) reported this species to be an uncommon migrant that had been observed in 12 (43%) of 28 degree blocks.

In 1984 three Herring Gull nests were located at Bamforth Lake, Albany County (B. H. Pugesek personal communication). This is the first record of this species breeding in Wyoming. One to three pairs of Herring Gulls continued to nest at Bamforth Lake in 1985 and 1986.

Although the Herring Gull has been reported from adjoining states of Colorado (Bailey and Neidrach 1965, Ryder 1978), Idaho (Larrison et al. 1967), Montana (Skaar 1980), Nebraska and South Dakota (Johnsgard 1979), and Utah (Behle and Perry 1975), I am unaware of breeding records from these states except for recent evidence of nesting at Antero Reservoir, Park County, Colorado (Chase 1987).

Glaucous Gull

The first record of the Glaucous Gull (*Larus hyperboreus*) in Wyoming is of a bird collected by E. Isberg at Lake Hattie, Albany County, on 23 November 1933 (McCreary and Mickey 1935, McCreary 1939). Another report of this species by A. B. Klots in McCreary (1930) was not mentioned later (McCreary 1939), possibly because the validity of the report was questionable.

There are three recent observations of the Glaucous Gull in Wyoming. On 23 September 1969, K. L. Diem observed one individual near Laramie, Albany County. A second Glaucous Gull was seen south of Laramie by W. Hepworth on 20 June 1979. The most recent report of this species from Wyoming is of a bird seen by O. K. Scott at Soda Lake, Natrona County, on 1 May 1982.

Few observations of Glaucous Gulls are expected in Wyoming because this species prefers coastal areas and large inland bodies of water and its breeding range is north of the contiguous United States (AOU 1983).

Black-legged Kittiwake

The Black-legged Kittiwake (*Rissa tridactyla*) was first reported in Wyoming by Knight (1902). One bird was collected by M. Jeserum near Douglas, Converse County, on 18 November 1898. Two more birds were observed at Dubois, Fremont County, on 22 October 1974 by M. Back (Kingery 1975). This is the only recent record of this species in Wyoming.

Because the Black-legged Kittiwake is primarily a pelagic species and breeds north of the contiguous United States (AOU 1983), only accidental occurrence is anticipated in Wyoming.

Sabine's Gull

McCreary (1939) indicated that the Sabine's Gull (*Xema sabini*) is rare in Wyoming. Two specimens were taken by A. E. Lockwood in the fall near lakes on the Laramie plains, Albany County (Grave and Walker 1913). Another Sabine's Gull was found dead near Douglas, Converse County, by K. Cook and A. Hay on 24 October 1937 (McCreary 1939).

Since 1954 there have been approximately 24 reports of Sabine's Gulls in Wyoming consisting of 28 individual birds. All sightings were made in September and October except for a subadult observed at Lake DeSmet, Johnson County, by J. Daly on 7 June 1981. The Sabine's Gull has been located in 7 (25%) of 28 latilong blocks and is considered a rare migrant in the state (Oakleaf et al. 1982).

According to the AOU Check-list of North American Birds (1983), the Sabine's Gull is primarily pelagic and breeds north of the contiguous United States. Thus, this species is expected to be seen rarely in Wyoming and then mostly during migration.

Caspian Tern

Skinner (1917) observed Caspian Terns (*Sterna caspia*) on the Molly Islands, Yellowstone Lake, Yellowstone National Park, but was unable to determine whether they were nesting. On 4 June 1932, Wright (1934) also saw this species on the Molly Islands and presumed it to be a breeder but failed to locate a nest. Kemsies (1930) first documented breeding Caspian Terns on the Molly Islands when he found eggs and downy young on 29 June 1929. Between 1932 and 1966 the number of Caspian Tern nests varied from a low of 4 nests on 5 July 1959 to a high of 18 on 24 June 1966 (Diem and Condon 1967). In 1955 Warkley found evidence of Caspian Terns nesting at Ocean Lake WHMA (Scott 1955). Also, McCreary (1939) indicated that A. B. Mickey located a pair on an island at Bamforth Lake, Albany County, in the summer of 1936. One nest of this species was discovered at Bamforth Lake in 1974, and two pairs appeared to nest there in 1975 (E. Raper personal communication). The most recent evidence of Caspian Terns nesting at Bamforth Lake is from 1983 when I counted four nests with eggs on 10 June. All nests were later destroyed by high water.

In recent years Caspian Terns have nested at five locations in Wyoming (Table 1). For unknown reasons, there has been a precipitous decline in the state's breeding population during recent surveys. The only active colony in 1985 and 1986 was at Pathfinder Reservoir.

Breeding records exist in Idaho (Larrison et al. 1967, C. H. Trost personal communication) and Utah (Behle and Perry 1975). I am unaware of nesting records in other states that adjoin Wyoming.

Common Tern

Bond (1885) was the first to list the Common Tern (*Sterna hirundo*) as occurring in Wyoming. This species was considered rare by both Knight (1902) and McCreary (1939). Two specimens were collected by McCarthy along the Sweetwater River, Natrona County, in 1859, and another bird was taken at Cheyenne, Laramie County, by F. Bond prior to 1902 (Knight 1902). Blackwelder may have seen a Common Tern in the Teton region (Grave and Walker 1913). Apparently, Woodbury (1937) collected a specimen at Yellowstone Lake, probably in 1931. Oakleaf et al. (1982) reported that the Common Tern was an uncommon summer resident in Wyoming, occurring in 9 (32%) of 28 latilong blocks. This species may occur in the state more frequently than reports indicate because of its similarity in appearance to the more common Forster's Tern.

Breeding records exist for the Common Tern in adjacent states of Idaho (C. H. Trost personal communication), South Dakota (Johnsgard 1979), and Montana (Skaar 1980).

Forster's Tern

Both Knight (1902) and Grave and Walker (1913) considered the Forster's Tern (*Sterna forsteri*) a rare migrant to be found only in the southeastern part of the state. McCreary (1939) indicated that this species was a common migrant in eastern Wyoming and summer resident in the southeastern portion of the state. One nest with two eggs was found on 31 May 1936 by A. B. Mickey at Bamforth Lake, Albany County, and a colony containing 12 nests was found at the same location on 2 July 1933 (McCreary 1939). Another nest of this species was discovered in Albany County as late as 21 July (McCreary 1939). Although Kemsies (1935) speculated that the Forster's Tern occurred fairly frequently in Yellowstone National Park and indicated that it may possibly breed in the marshes bordering Yellowstone Lake, thus far there has been only one record for the park.

Oakleaf et al. (1982) considered the Forster's Tern a common summer resident and reported it as a breeding species from one (3.6%) latilong and occurring in 20 (71%) of 28 latilongs. During the 1982–86 period, Forster's Terns

TABLE 1. Location, number of nests, and habitat of Caspian Tern colonies in Wyoming, 1983–86.

Name	Location	Number of nests 1983	1984	1985	1986	Habitat
Albany County						
Bamforth Lake						Lake
Bamforth Island	41°24′N,105°44′W	4	0	0	0	
Carbon County						
Pathfinder Reservoir						Reservior
Bird Island	43°23′N,106°56′W	NC[a]	15–20	23	29	
Natrona County						
Soda Lake						Reservoir
West Island	42°54′N,106°19′W	13	0	0	0	
Rattlesnake Island	42°54′N,106°18′W	0	1	0	0	
Yellowstone National Park[b]						
Yellowstone Lake						Lake
Molly Islands	44°19′N,110°16′W	12	3	0	0	

[a]NC = not censused.

[b]Data from K. L. Diem (personal communication).

TABLE 2. Location, number of nests, and habitat of Forster's Tern colonies in Wyoming, 1982, 1984–86.

		Number of nests				
Name	Location	1982	1984	1985	1986	Habitat
Albany County						
Caldwell Lake	41°09′N,105°48′W	NC[a]	NC	NC	19	Lake
Carroll Lake	41°25′N,105°44′W	NC	NC	15–20	3	Lake
Hutton Lake NWR	41°11′N,105°44′W	8–15	0	3	2–3	Marsh
Kay Ranch	41°15′N,105°42′W	2–3	0	0	0	Lake
Pilger Lake	41°23′N,105°50′W	NC	NC	NC	9	Lake
Fremont County						
Ocean Lake	43°07′N,108°35′W	NC	10	36	12	Reservoir
Lincoln County						
Bear River	42°01′N,110°58′W	0	2–3	0	0	Marsh

[a] NC = not censused.

nested at seven locations in Wyoming (Table 2). However, not all of these sites were active each year. Based on the 1986 colony censuses, approximately 45–46 nests were present. This compares to 10–18 active nests in two colonies during 1982. The increase in the breeding population is primarily a result of locating four new nesting areas during recent surveys. I am uncertain why Forster's Terns failed to nest on the Kay Ranch and Bear River in 1985 and 1986. Significant declines in nesting Forster's Terns were also noted at Ocean Lake and Carroll Lake in 1986. Fewer terns probably nested at Carroll Lake because of very low water levels that reduced nesting habitat. At Ocean Lake the decline may have been caused by the addition of more cobble to the man-made nesting islands, which made them more dome-shaped and less suitable as nesting substrate. Flooding of nests may also be a serious problem at Ocean Lake.

Breeding records exist for this species from adjoining states of Colorado (Bailey and Neidrach 1965), Idaho (Larrison et al. 1967, C. H. Trost personal communication), Montana (Skaar 1980), Nebraska and South Dakota (Johnsgard 1979), and Utah (Behle and Perry 1975).

Least Tern

McCreary (1939) indicated that the Least Tern (*Sterna albifrons*) was a summer resident along the North Platte River. The first sighting of this species was at Torrington, Goshen County, on 11 June 1929 (McCreary 1934, McCreary and Mickey 1935). J. W. Scott noted 8 or 10 individuals near Fort Laramie, Goshen County, on 25 June 1932 (McCreary 1934). One year later on 27 May the Least Tern was again reported from Torrington, Goshen County (McCreary 1939). No recent records exist in the state for this species.

The Least Tern breeds locally and irregularly in South Dakota and Nebraska (Johnsgard 1979). I am unaware of nesting records from other states that are adjacent to Wyoming.

Black Tern

Bond (1885) was the first to list the Black Tern (*Chlidonias niger*) as occurring in Wyoming. This species was considered a rare migrant in the state by Knight (1902). Grave and Walker (1913) indicated that there were records of Black Terns from Cody, Park County; Sheridan, Sheridan County; Lake Como, Albany County; Cheyenne, Laramie County; and Douglas, Converse County. McCreary (1939) noted this species as being a common migrant in eastern Wyoming and a summer resident in the southeastern portion of the state. Henninger (1915) found a nest containing one egg near Bamforth Lake on 12 June 1914. This was the first documentation of nesting by Black Terns in Wyoming. In Yellowstone National Park, Kemsies (1930) reported that the Black Tern was a frequent migrant and probable summer resident. This species is considered a common summer resident by Oakleaf et al. (1982) and has been reported from 20 (71%) of 28 latilong blocks with strong evidence of breeding from 2 latilongs. On 3 June 1982, I discovered 2–4 nesting pairs of Black Terns with eggs on the Kay Ranch, about 10 km southwest of Laramie, Albany County. From 1984 through 1986 this species nested at three locations in Albany County and in the marshes associated with the Bear River, south of Cokeville, Lincoln County (Table 3). Since 1984, new Black Tern colonies have been discovered at Carroll and Caldwell

TABLE 3. Location, number of nests, and habitat of Black Tern colonies in Wyoming, 1984–86.

Name	Location	Number of nests 1984	 1985	 1986	Habitat
Albany County					
Caldwell Lake	41°09′N,105°48′W	NC[a]	NC	2–3	Lake
Carroll Lake	41°25′N,105°44′W	NC	10–15	2–3	Lake
Hutton Lake NWR	41°11′N,105°44′W	7–10	8–10	1–2	Marsh
Kay Ranch	41°15′N,105°42′W	0	0	0	Lake
Lincoln County					
Bear River	42°01′N,110°58′W	100–150	NC	NC	Marsh

[a]NC = not censused.

lakes. For unknown reasons, this species failed to nest at the Kay Ranch during the 1984–86 period and has not been documented as breeding there since 1982. Population trends of Black Terns are unknown in Wyoming because most colonies have been monitored an insufficient number of years. Also, numbers of Black Terns nesting in the marshes adjoining the Bear River have not been censused since 1984.

This species has been found nesting in the following states that adjoin Wyoming: Colorado (Bailey and Neidrach 1965), Idaho (Larrison et al. 1967, C. H. Trost personal communication), Montana (Skaar 1980), Nebraska and South Dakota (Johnsgard 1979), and Utah (Behle and Perry 1975).

CONCLUSIONS

In recent years observations of nonbreeding species of gulls, terns, and jaegers have increased in Wyoming. I believe these increases are primarily a result of more surveys being conducted by professional biologists and more time spent in the field by greater numbers of amateur birdwatchers. Of the 11 nonbreeding Laridae documented in the state, the Pomarine Jaeger and Heermann's Gull were reported for the first time since 1980. Also, the majority of sightings of other nonbreeding species have occurred during the last 10–15 years. Observations of these species will most likely continue to increase as more individuals take up birdwatching as a hobby in Wyoming. Alternative explanations for increased reports of nonbreeding species of Laridae are range expansions or changes in migration routes. I am unaware of evidence from Wyoming or elsewhere for either explanation.

It is unknown whether breeding populations of some Laridae in Wyoming have recently increased or whether new colonies are the result of intensive surveys. I believe that evidence exists for recent population increases of the Ring-billed Gull, California Gull, and Herring Gull in the state. Reasons for proliferation of California Gull, and possibly Ring-billed Gull and Herring Gull, populations in Wyoming include construction of large reservoirs with isolated islands for nesting as well as creation of new food sources such as garbage dumps, other human refuse, and agricultural land (Findholt 1986a). Breeding populations of these species apparently are expanding throughout the western United States (Conover 1983, Chase 1987). In contrast, I believe most new colonies of Caspian Terns, Forster's Terns, and Black Terns are a result of current surveys, and not the result of recent breeding range expansions into Wyoming. However, the addition of at least a few new colonies of Caspian Terns and Forester's Terns in Wyoming since historical times appears to be the result of human-caused environmental changes, especially the construction of reservoirs, which have created nesting and foraging habitat.

With the exception of the California Gull, which is a relatively abundant and widespread nesting species in Wyoming, breeding populations of the other five species of Laridae that nest in the state are small. It appears that limited nesting and foraging habitat restricts population sizes of most gulls and terns. Also, because Wyoming is at the edge of the breeding range of most species currently nesting in the state, populations may remain small.

It seems unlikely that nesting populations of the 11 nonbreeding Laridae will be documented in Wyoming, except for the Franklin's Gull and Common Tern, because the breeding range of most species occurs along coastal areas or north of the contiguous United States. The only other species, in addition to the

Franklin's Gull and Common Tern, that nests in states that adjoin Wyoming is the Least Tern. Since the Least Tern nests locally and irregularly in South Dakota and Nebraska and does not appear to be expanding its range, it seems unlikely that it will be found nesting in Wyoming (Johnsgard 1979).

It is difficult to assess long-term population trends of most Laridae that currently breed in Wyoming because of the limited number of years that population data are available. However, results presented in this paper will serve as baseline data that can be used to evaluate future population changes in the state.

Because most breeding colonies are currently protected in Wyoming, prospects for maintaining viable nesting populations appear good. It is my hope that natural resource management agencies will continue efforts to monitor long-term population changes and will implement appropriate management strategies to ensure that currently unprotected breeding populations of Laridae are maintained in the state.

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SEED PRODUCTION IN *GENTIANA NEWBERRYI* (GENTIANACEAE)

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ABSTRACT.—Experimental manipulations and observations in one population of *Gentiana newberryi* Gray flowers over 2 years showed significant variation in seed production relative to pollinator and soil water availability. When pollinators were rare, there was a significant relationship between number of bees present and number of mature seeds produced, and supplemental hand cross-pollination (xenogamy) did improve seed set in *Gentiana newberryi* Gray. When pollinators were abundant, supplemental hand cross-pollination did not increase seed set. Self-fertilized seeds (autogamy) germinated at the same rate as cross-pollinated seeds. Seed production in unvisited flowers is probably limited anatomically and is not influenced by the type of fertilization. There was a significant relationship between soil moisture and flower size in *G. newberryi,* with larger flowers found in wetter areas.

Key words: Gentiana, *seed production, pollination, bumblebees, soil water potential.*

Seed set can be limited by insufficient pollinator visits (Levin and Anderson 1970, Thomson 1980, 1981, Bierzychudek 1981, Gross and Werner 1983, Pleasants 1983, Waser 1983a, Motten 1986, Galen and Newport 1988, Calvo and Horvitz 1990, Harder 1990, Ashman and Stanton 1991) or by other resources, such as water or nutrients, in populations with sufficient pollinators (Stephenson 1981, Evenson 1983, McDade and Davidar 1984, Primack and Kang 1989). Resource limitation may result in aborting the whole fruit or only some seeds in a fruit (Lee 1988). Multiple reproductive strategies in perennials, including cross-pollination, self-compatibility (Levin 1971, Jain 1976, Barrett 1988, Karoly 1992), and vegetative reproduction (Evenson 1983, Waller 1988), are advantageous in populations where pollinators and other resources are un-predictable (Motten 1982, Sutherland 1986, Ehrlen 1992). While self-fertilized and vegetatively produced plants increase the risk of inbreeding depression, those that are successful may have coadapted genes that are advantageous for current environmental stresses (Lloyd 1979, Waser and Price 1982, Barrett 1988).

Optimal flowering time is when a plant can attract the most visitors and still be able to set seed during the growing season (Pleasants 1983, Waser 1983b, Primack 1987). When bees are abundant, pollination does not limit seed set. When bees are infrequent, there is often a correlation between seed set and pollinator visitation rate (Zimmerman 1980, McDade and Davidar 1984, Zimmerman and Pyke 1988). Supplemental hand pollination can be used to determine whether pollinators or climatic factors are limiting seed set (Motten 1983).

Here we present both observational and experimental data on seed production in *Gentiana newberryi* Gray. These perennial plants are restricted to high-elevation wet meadows in eastern California, western Nevada, and southern Oregon (Munz 1973). *Gentiana newberryi* has protandrous, funnel-shaped flowers that are usually white with greenish spots (Munz 1973). Each ramet has one or two flowering shoots with one or two terminal flowers (personal observation). They can reproduce sexually and vegetatively (Spira 1983, Spira and Pollak 1986).

Initial observational data included pollination mode, pollinator activity, and soil moisture effects on seed production. Based on observational information, we then measured soil water potential and pollinator visitation across the study area and throughout the season to determine relationships between pollinator availability or soil moisture and seed production.

METHODS AND MATERIALS

Study Site

In August 1991 we selected a 2700-m^2 study site at Little Valley, 27.3 km southeast of

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Reno, Nevada (119°52′W, 39°15′N). The site, located at an elevation of 2000 m along the eastern edge of the Sierra Nevada escarpment, is part of the 1200-ha Whittell Forest and Wildlife Area owned by the University of Nevada, Reno (Rust 1987). The area is covered by snow each winter but has an average of 120 days with minimum temperatures above 0°C (Houghton et al. 1975). *Gentiana newberryi* populations are found in meadows that collect and retain snowmelt water longer than surrounding meadow areas. A small creek running through the southern portion of the site keeps the areas near the creek wet throughout the growing season. Central and northern portions of the site dry out toward the end of the growing season. The study was conducted during the fifth and sixth years of a drought when snowfall was only 50% of normal (James 1992). Most flower species began flowering 4 weeks earlier than usual in 1992 (personal observation) after a warm spring and early snowmelt (James 1992).

Population Characteristics

In mid-September 1991 and 1992, numbers of plants (ramets) and flowers on the study site were estimated using 11 transects (38–54 m long) placed 5 m apart and extending across the population to include all *G. newberryi* plants. At each meter along each transect all plants and flowers were counted and percentage of *G. newberryi* coverage was estimated within 0.5-m^2 circular quadrats.

Floral Characteristics

In 1992, after observing the differential drying of the study site in 1991, we divided the site into five areas. Area 1 was adjacent to the southern creek (always wet during 1991). Areas 2 to 5 were equally spaced away from the creek, with area 2 the closest to area 1 and area 5 the farthest removed. Soil water potential was measured in each area weekly with a Quickdraw Series 2900 Soil Moisture Probe. Moisture was measured at approximately 30 cm. Three measurements were taken per area per week. Petal length and maximum corolla tube width were measured for 10 random *G. newberryi* flowers (each from a different plant, and with dehiscing anthers) in each area in 1992 (n = 50). An index was developed to compare flower size by multiplying petal length by corolla tube width. Ultraviolet reflectiveness was determined by photographing numerous buds and open flowers on live plants in the field with a Wratten 18A UV filter.

On 21 August 1991, 10 mature bud flowers (ready to open) were marked and covered with waxed paper bags (1 in the wet area and 9 in the dry). Another 13 buds were marked and left uncovered (7 in the wet and 6 in the dry area). At 0900 the following morning, nectar volume in each flower was measured using a 1-μl capillary tube. On 13 September 1991, 10 mature bud flowers in the dry area and 13 in the wet area were bagged. The following afternoon (1300) nectar was measured from each flower. Each week during 1992 nectar was measured at approximately 0900 from one randomly selected, uncovered, dehiscing flower in each of the five soil moisture areas (n = 60).

Pollinators

Bumblebees were common throughout August and September 1991, but the number of bees present was not regularly recorded. Individual foraging bees were followed; and the flowers visited, distance between flowers, and times were recorded. In 1992 a 100-m transect was established across the drier part of the site and a 50-m (shorter due to limits of the wet area) transect placed across the wet area. These transects were walked hourly at least 2 days each week, and any bees observed within 5 m of the transect were recorded. A sample of all insect visitors to *G. newberryi* was collected for identification by R. Rust, University of Nevada, Reno, and R. Brooks, University of Kansas, Lawrence.

Seed Production

In 1991 flower buds of *G. newberryi* were randomly selected with not more than one flower per plant and marked with numbered paper tags (n = 113). Three times each week the phenology (bud, flower opening, dehiscing anthers, receptive stigma, and seed capsule formation) of each marked flower and soil moisture conditions adjacent to the plant (visually) were recorded. During 1992 two newly opened flowers on different plants with dehisced anthers in each area were randomly selected and marked each week from early July through early October (n = 84). Mature seed capsules for all marked flowers were collected and placed in individual waxed paper bags. Mature seeds and undeveloped ovules were counted using a dissecting microscope. Seeds for each flower with any mature seeds were placed in individual waxed paper bags and stored outdoors in Reno, Nevada.

During August 1991, 53 *G. newberryi* buds were randomly selected and marked, and the plants covered with white nylon organdy (100-mesh) bags over wire frames. When the flowers opened, 9 were hand-pollinated using a paint brush bearing pollen from a flower on the same plant (geitonogamy), 12 with pollen from a different plant (xenogamy), and 34 were left to self-pollinate (autogamy). During the week of 18 August 1992, 10 plants (2 in each soil moisture area) with bud flowers were selected at random, marked, covered with nylon organdy bags, and allowed to self-pollinate. Ten other newly opened flowers in the different areas were marked and cross-pollinated by hand after the stigma became receptive. Another 10 flowers in the different areas were marked and left alone for natural pollination. Mature seed capsules for treatments used in 1991 and 1992 were collected and seeds counted and stored using the same method.

Each year five randomly chosen seed capsules from each treatment and the open flowers were germinated. Seeds for each flower were placed in a petri dish on brown paper over kimpack moistened with a 400 ppm giberellic acid solution. Seeds were kept at 15°C for 7 d and then alternated between 15°C for 12 h and 25°C for 12 h for 7 d in the dark.

Statistical Analyses

Analysis of variance (GLM in SAS 1990) was used for all comparative analyses between years and between areas or weeks within each year. Bonferroni t tests were used for multiple comparisons when analysis of variance indicated a significant difference. Arcsine transformations were used for analysis of percentage data (Zar 1974). Linear regression (SAS 1990) was used to determine if there was a relationship between soil moisture and flower size, soil moisture and seed production, or seed production and bee visits each week. Plant distribution was determined using the standardized Morisita index (I_p; Krebs 1989).

RESULTS

Population Characteristics

There was no significant difference between 1991 and 1992 in number of plants (F = 0.43, df = 1,984, P = .51) or number of flowers (F = 1.16, df = 1,984, P = .28) per quadrat (Table 1). Percentage cover was significantly different between years (F = 3.97, df = 1,984, P = .04) (Table 1). Distribution of plants is clumped throughout the study site as indicated by the Morisita index (I_p = 0.51).

Floral Characteristics

A significant difference in *G. newberryi* flower size (petal length × maximum corolla tube width) was found among the five soil moisture areas of the study site in 1992 (F = 37.04, df = 4,45, P < .0001; Table 2). There was a significant regression ($y = 693.4 + 12.5x$) between soil water potential and flower size (F = 117.79, df = 1,48, P < .0001; R^2 = .71), with larger flowers found in wetter areas.

Ultraviolet images of *G. newberryi* flowers show a dark, central, UV-absorbing bullseye pattern in the corolla tube and a dark longitudinal stripe on the outside of each petal from the base to the apex. Outer petal stripes are also visible on flower buds.

In 1991, in a sample of newly opened flowers at 0900 h, there was no difference in the amount of nectar available between flowers covered with a bag overnight (0.1 ± 0.1 [mean and standard deviation], range 0–0.3 μl) and those left open (0.1 ± 0.1, range 0–0.3 μl) (F = 0.03, df = 1,22, P = .97) or in the amount of nectar in flowers between wet area (0.4 ± 0.4, range 0–1.4 μl) and dry area (0.2 ± 0.2, range 0–0.7 μl) (F = 2.02, df = 1,21, P = .17). In 1992 there was no difference in the amount of nectar available in open flowers between

TABLE 1. Number of *G. newberryi* plants, flowers, and percentage of cover per 0.5-m² quadrat at Little Valley, Nevada. Values are means ± standard deviation; n = 493. Total numbers of plants and flowers in 2700-m² study site are in parentheses.

Plants (no.)	Flowers (no.)	Percent cover
	1991	
1.2 ± 3.7 (3115)	2.3 ± 3.1 (773)	1.7 ± 5.5
	1992	
1.1 ± 4.1 (2710)	0.2 ± 1.1 (476)	1.1 ± 5.4

TABLE 2. Relationship between soil water potential and flower size in *G. newberryi* at Little Valley, Nevada, in the second week of July 1992. Soil water potential, petal length, corolla width, and a flower size index (petal length × corolla width) are indicated for five areas of decreasing soil water potential. Values are means ± standard deviation; $n=10$.

Area	Soil water potential (MPa)	Petal length (mm)	Corolla width (mm)	Flower size index	
1	0.0 ± 0.0	46.5 ± 2.4	16.4 ± 1.0	764.1 ± 79.0	A[a]
2	–3.5 ± 0.5	44.0 ± 3.5	14.0 ± 1.8	617.6 ± 106.8	B
3	–6.0 ± 1.6	41.7 ± 3.6	13.3 ± 1.9	557.7 ± 105.5	B
4	–12.0 ± 4.9	38.3 ± 3.1	11.0 ± 1.9	425.1 ± 102.3	C
5	–35.0 ± 0.0	33.1 ± 2.9	8.6 ± 1.8	287.5 ± 74.4	D

[a] Bonferroni *t* tests comparing differences in flower size index among areas. Means with the same letter are not significantly different ($P < .05$).

weeks (week 1—0.1 ± 0.1, range 0–0.3 μl; week 2—0.6 ± 0.9, range 0–2.1 μl; week 3—0.4 ± 0.3, range 0–0.7 μl; week 4—0; week 5—0.7 ± 0.4, range 0.4–1.3 μl; week 6—0.1 ± 0.2, range 0–0.4 μl; and week 7—0.2 ± 0.2, range 0–0.4 μl) (F = 1.99, df = 6,28, P = .10). No difference in amount of nectar was found between areas (area 1 [driest]—0.1 ± 0.2, range 0–0.5 μl; area 2—0.3 ± 0.2, range 0–0.6 μl; area 3—0.2 ± 0.3, range 0–0.7 μl; area 4—0.4 ± 0.4, range 0–1.3 μl; and area 5 [wettest]—0.6 ± 0.8, range 0–2.2 μl) (F = 1.01, df = 4,30, P = .41). Most nectar was usually found in one or two of the five nectar tubes.

Pollinators

In 1991 four species of bumblebees were observed visiting *G. newberryi* flowers (Table 3). Most visits were for nectar. Nectar foragers would pick up pollen on their ventral surface from the centrally located anthers. *Bombus appositus* Cresson and *Bombus edwardsii* Cresson were frequent visitors to *G. newberryi* from early August until the end of September. *Bombus vosnesenskii* Radoszkowski was frequently observed visiting *Lupinus sellulus* Kell. adjacent to *G. newberryi* and occasionally visited a few *G. newberryi* flowers. *Bombus fervidus* (Fabricius) was seen visiting *G. newberryi* flowers during only one week in August. Usually between one and six bumblebees could be found visiting *G. newberryi* flowers on the study site anytime during August and September when the weather was warm and calm.

During 1992, bumblebee visits to *G. newberryi* were rarely observed. A few visits by *Bombus edwardsii* were seen. *Bombus vosnesenskii* were observed visiting other flower species and occasionally robbed nectar from *G. newberryi* from outside the flower. *Anthophora bomboides* Kirby, *A. urbana* Cresson, and *A. terminalis* Cresson were occasionally observed visiting *G. newberryi*. *Apis mellifera* L. were common visitors to adjacent *Lupinus sellulus*, and one was seen visiting a *G. newberryi* flower. *Anthophora* species and *A. mellifera* were not seen in 1991.

In 1992 there were always many flowers open with pollen available. Less than one bee per 750 m^2 was observed when walking transects. There was a significant positive correlation between number of bees observed each week along the combined transects and number of seeds produced per flower marked that week (Fig. 1).

Seed Production

There was no significant difference in the mean number of mature *G. newberryi* seeds produced per marked flower between 1991 (116.2 ± 143.6, n = 58) and 1992 (135.4 ± 114.4, n = 76) (F = 0.75, df = 1,132, P = .38). When we eliminated flowers with aborted seed capsules from the analysis (50% aborted 1991, 23% 1992), the number of mature seeds per capsule was higher in 1991 (232.4 ± 118.3, n = 29) than 1992 (174.6 ± 100.0, n = 59) (F = 5.76, df = 1,86, P = .01).

In 1991 significantly more seeds were produced by *G. newberryi* flowers in the areas with a wet soil surface (210.3 ± 175.1, n = 20) than in the dry areas (66.7 ± 93.4, n = 38) (F = 16.70, df = 1,56, P < .0001). More seed capsules aborted in the dry than the wet area

TABLE 3. Total number of visits, mean length of visits, and mean distance traveled between flowers for varying numbers of individuals of four foraging *Bombus* species at Little Valley, Nevada, in August 1991. Values for time and distance are mean ± standard deviation.

Species	Individuals	Visits	Time (sec)	Distance (cm)
B. appositus	1	6	10.3 ± 0.7	13.5 ± 8.3
B. edwardsii	1	20	12.8 ± 4.5	9.1 ± 24.7
B. fervidus	5	45	14.7 ± 9.2	64.4 ± 98.2
B. rosnesenskii	3	26	8.2 ± 5.6	23.5 ± 23.2

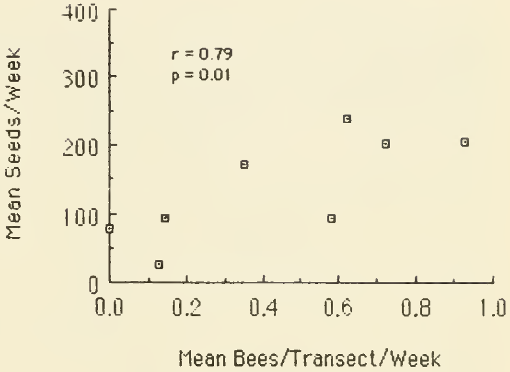

Fig. 1. Correlation between mean number of bees observed along combined transects and mean number of seeds produced by *G. newberryi* flowers that were open the week bees were observed; $n = 7$.

(58% vs. 35%). A higher percentage of ovules per capsule matured to seed in the wet area (84.7 ± 10.8%, $n = 13$) than in the dry area (60.2 ± 24.0%, $n = 16$) ($F = 5.88$, df = 1,27, $P = .01$).

In 1992 there was no significant difference in the number of mature seeds produced per flower between the areas with varying soil water (area 1 [driest]—133.7 ± 112.5, area 2—153.1 ± 98.4, area 3—57.0 ± 79.3, area 4—161.9 ± 135.8, and area 5 [wettest]—142.1 ± 122.8) ($F = 2.26$, df = 4,79, $P = .07$) or in the percentage of ovules that matured to seed per capsule ($F = 0.56$, df = 4,60, $P = .69$). There was, however, a significant positive relationship between soil water at the time a flower opened and number of mature seeds produced ($y = 158.9 - 2.3x$ and $F = 5.96$, df = 1,69, $P = .02$).

There was a significant difference in the average number of seeds produced ($F = 8.44$, df = 3,83, $P < .0001$) and the percentage of ovules that matured to seeds ($F = 9.06$, df = 3,42, $P < .0001$) between the open, xenogamous, and geitonogamous versus autogamous pollination treatments in 1991 (Table 4). In 1992 there was also a significant difference between pollination treatments of open and xenogamous versus autogamous in the average number of seeds produced ($F = 11.37$, df = 2,20, $P = .0005$) and the percentage of mature seeds per capsule ($F = 8.15$, df = 2,25, $P = .002$) (Table 4). Hand cross-pollinated (xenogamy) seed production was highest but was not statistically different from open bee pollination in both years. Autogamous seed production was lowest but not statistically different from open pollination.

The percentage of germinated *G. newberryi* seeds was not significantly different between treatments in 1991 ($F = 2.00$, df = 3,15, $P = .15$) or 1992 ($F = 2.93$, df = 2,9, $P = .10$). Seed germination ranged from 91.5 to 98% in 1991 and 84.8 to 98.8% in 1992 for all treatments.

DISCUSSION

Seed production per marked *Gentiana newberryi* flower was not significantly different between 1991 and 1992 in Little Valley, even though pollinator numbers and soil moisture were different between the 2 years. The large variation observed in all measurements of *G. newberryi* population characters and flower/seed characters in the Little Valley population both among and between years suggests much individual variability. Within the *G. newberryi* habitat area, individuals respond to a variety of localized microenvironmental parameters with the resulting variation in sexual reproductive output.

Bumblebees visiting *G. newberryi* were abundant during 1991. It is unlikely that pollinators limited seed set in 1991 since flowers with hand cross-pollination did not set significantly more seeds. There was a higher number of aborted fruits in the dry area in 1991. During 1992, when soil was wetter, *G. newberryi* plants appeared more vigorous throughout the study area. Low pollinator availability in 1992 did appear to limit seed set, as the number of flowers that matured seeds each week was correlated to the number of bees observed. Zimmerman (1980) and McDade and Davidar (1984) both found that seed set was correlated with visitation rates when pollinator numbers

TABLE 4. Percentage of mature seeds per capsule and number of mature seeds per flower in four pollination treatments. Treatment 1 = open, 2 = hand cross-pollinated, 3 = self-pollinated, 4 = hand-pollinated from flower on same plant. Aborted seed capsules were not included in the percentage of mature seeds per capsule analysis. Values are mean ± standard deviation; *n* is in parentheses.

Treatments	Mature seeds per capsule (%)				Mature seeds per flower (no.)			
				1991				
1	72.5 ± 25.2	(16)	A[a]		124.3 ± 155.8	(32)	A	B
2	69.9 ± 27.8	(12)	A		189.6 ± 91.6	(12)	A	
3	22.5 ± 23.6	(11)		B	20.4 ± 49.5	(34)		B
4	49.3 ± 34.0	(7)	A	B	105.6 ± 130.0	(9)	A	B
				1992				
1	58.5 ± 27.5	(6)	A	B	93.8 ± 94.7	(8)	A	B
2	90.8 ± 8.0	(10)	A		156.5 ± 35.3	(10)	A	
3	45.9 ± 24.8	(7)		B	46.0 ± 42.5	(10)		B

[a] Bonferroni *t* tests comparing treatments within each year. Means with same letter are not significantly different ($P < .05$).

were low. When aborted fruits were eliminated from the analysis in 1991 (50%), more mature seeds were produced per flower in 1991 than in 1992. This also suggests that the larger number of bees present in 1991 increased the numbers of seeds produced in plants with sufficient moisture to produce mature fruits. Fruit initiation may be pollinator limited, but mature fruit and seed production are primarily limited by resources such as water (Galen and Newport 1988, Horvitz and Schemske 1988, Ashman and Stanton 1991).

It is not known whether the rarity of bees observed in 1992 could be related to drought conditions or snow and cold weather in late June. Many species of bees were seen foraging on other flower species in Little Valley during May 1992 (personal observation). Numerous male *Bombus vosnesenskii* were observed foraging on several flower species on the study site during July, but few females of any *Bombus* species were seen during the *G. newberryi* flowering period. In contrast, an open flower in 1991 could rarely be found with pollen remaining on the anthers. Throughout 1992, most open *G. newberryi* flowers had nectar and abundant pollen available as potential pollinator rewards.

There were large populations of *Lupinus sellulus* adjacent to patches of *G. newberryi*, and Aster species and *Perideridia bolanderi* (Gray) Nels. & Macbr. were common from July through September. In 1991 *Bombus edwardsii*, *B. fervidus*, and *B. appositus* were seen visiting only *G. newberryi*. *Bombus vosnesenskii* was usually observed visiting *L. sellulus* with occasional visits to several *G. newberryi*. In 1992 the few bees observed visited a variety of flowers, and none showed a preference for *G. newberryi*. We observed a few nectar-robbing visits from outside the flower by male *B. vosnesenski* in 1992.

Ultraviolet markings in the center of the corolla and on the outside of petals attract and guide bees to nectar sources (Silberglied 1979, Kevan 1983, Waddington 1983, Waser 1983b). Bumblebees were often observed flying quickly and directly in a straight line from *G. newberryi* flower to flower. When entering a flower, a nectar-foraging bee positions its ventral surface over the anthers in the staminate phase and over the stigma in the pistillate phase. Bees were rarely observed collecting *G. newberryi* pollen.

There was no difference in the rate of seed germination between self- and cross-pollinated flowers. Seed production is not affected by type of pollination, but it may be limited anatomically in unvisited self-pollinated flowers. As the flower closes, the stigma bends over and touches only one or two of the anthers. Caged plants that were hand-pollinated with pollen from a flower on the same plant produced as many seeds as open plants or plants with supplemental hand cross-pollination.

Plants in wetter soil had larger, showier flowers than those in dry soil. Pollinators are usually attracted to larger flowers (Galen and Newport 1988, Ashman and Stanton 1991). In 1991 the surface soil was very dry in a large part (1800 m^2) of the study site. Fewer seeds matured per flower and more seed capsules aborted in the dry area, suggesting that inadequate soil water can limit the number of seeds produced per flower. Surface soil throughout the study site appeared wetter in 1992. The positive relationship between soil water at flower opening and number of mature seeds produced in 1992 indicates the importance of sufficient water resources in determining seed set.

Facultative self-compatibility allows *G. newberryi* to produce seeds even when pollinators are rare. Vegetative reproduction requires less energy (Waller 1988) and may be used in addition to or in place of flower production or sexual reproduction. Of 10 plants that were dug up, only one did not have an attached lateral rhizome. Since data will continue to be collected from this site, we did not dig up a sufficient number of plants to be able to determine size of clones or average number of rhizomes per ramet.

There was no significant difference in population size, number of flowers, or mean number of seeds produced per flower between 1991 and 1992. Some plants marked in 1991 that remained covered with 1 cm of water or more from the natural creek diversion did not survive.

Larger *G. newberryi* flowers are found in wetter areas and produce more mature seeds than flowers in drier soil areas. There was a significant relationship between number of pollinators present and number of seeds produced only when pollinators are rare. There was no difference in seed production between flowers with xenogamous and geitonogamous pollination. Facultative self-compatibility and vegetative reproduction allow plants to produce seeds or ramets when pollinators are limiting. *Gentiana newberryi* appears well adapted to survive during unpredictable periods of pollinator availability and soil moisture.

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USE OF A SECONDARY NEST IN GREAT BASIN DESERT THATCH ANTS (*FORMICA OBSCURIPES* FOREL)

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ABSTRACT.—Workers of Great Basin Desert thatch ants (*Formica obscuripes* Forel) dig simple secondary nests at the base of plants upon which they tend aphids and scales. These secondary nests house only foragers, with the number of foragers occupying each nest positively correlated with the number of worker-tended Homoptera feeding on plant foliage above. Thatch ant secondary nests are cooler than 25 cm below the dome top of the primary nest and maintain a significantly more constant temperature than is observed on the ground surface or in the plant canopy. Thatch ant foragers use secondary nests for at least two purposes: as a cool refuge for Homoptera tenders when midday plant canopy temperatures rise during the summer months, and as the primary place within which Homoptera tenders transfer honeydew to larger "honeydew transporters" for ultimate transport back to the primary nest.

Key words: honeydew harvest, thermal refugia, behavioral thermoregulation, red wood ants, desert adaptation, satellite nests.

Although most ant species use a nest structure consisting of a single central location (a primary nest), many species also employ "secondary" nests in which a portion of the colony population is dispersed among several alternate sites (Wheeler 1910).

Several species of *Camponotus*, for example, use a secondary nest to which workers transport late-instar larvae and pupae from a central location occupied by the queen and brood (Hansen and Akre 1987). Similarly, the dolichoderine *Iridomyrmex sanguineus* maintains secondary nests containing older larvae and pupae, but workers bring young from several locations within oligogynous colonies (McIver 1991).

Many other ant species (*Polyrachis simplex, Lasius niger, L. emarginatus, Formica pratensis, F. exsectoides, Crematogaster pilosus*) are known to use secondary nests in which only foraging workers reside (Forel 1921, Andrews 1929, Ofer 1970). These secondary nests are thought to serve as refuges for the workers from the physical environment, as a defense against enemies, or as a protected site within which to tend Homoptera for honeydew (Wheeler 1910).

This paper characterizes the secondary nest used by the thatch ant *Formica obscuripes* Forel living in the Great Basin Desert and discusses its possible function within the context of the desert environment.

STUDY AREA AND SPECIES

Thatch ants were studied between June 1987 and September 1991 at Pike Creek, 160 km southeast of Burns, Oregon. The Pike Creek study site is at 1300 m elevation at the base of Steen's Mountain in the northern Great Basin Desert. Sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus nauseosus*), horsebrush (*Tetradymia* sp.), lupine (*Lupinus caudatus* Kellogg), and cheatgrass (*Bromus* spp.) are dominant plants at the site, which was grazed moderately by cattle throughout the study period.

A total of four colonies of *Formica obscuripes* Forel were observed for various parts of the study. *F. obscuripes* is a widespread and abundant North American *rufa*-group species (Wheeler and Wheeler 1983). Like *F. rufa*-group species elsewhere, *F. obscuripes* builds symmetrical, dome-shaped primary nests of thatch, from which radiate trunk trails that access foraging territory. In all four study colonies workers foraged for honeydew on sagebrush, rabbitbrush, horsebrush, and/or lupine, and scavenged for arthropods in the area surrounding each nest. Although broodless satellite nests were occasionally observed, there was no evidence of primary nest polydomy in any study colonies.

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METHODS AND MATERIALS

Secondary Nest Characteristics

The aboveground structure of the secondary nest is portrayed by a photograph taken from colony 5 at Pike Creek, August 1988. The belowground structure was investigated by pouring a measured quantity of dental labstone down 10 different secondary nest entrances of two colonies (colonies 4 and 26) during August 1991. Quantity of labstone required to fill each secondary nest was then correlated with basal plant diameter and number of workers tending Homoptera in the plant canopy. Actual structure of the secondary nest interior was determined by excavating two nests, photographing the labstone "plug" in place, and drawing one of these to scale using the photograph as reference.

Temperature at 6 cm depth in a typical secondary nest (plant A, colony 2) was measured during summer 1987 and compared to measurements for tending localities in the plant canopy, ground surface, and 25 cm below the top of the primary nest dome.

Secondary Nest Use

Use of the secondary nest by thatch ant workers was explored by conducting intensive observations on a selected sagebrush plant (plant 13) at the Pike Creek study site during July 1987. Beginning 1 July 1987, thatch ants working in the vicinity of plant 13 were individually marked with "beenumbers" (Charles Graz Co., Frankfurt, Germany) so that the activity pattern of each could be determined. By 23 July, a total of 66 workers had visited plant 13 and been marked, 30 of which were still using the plant daily. At noon on 23 July, we began a 24-h continuous period of observation of worker behavior on plant 13. We recorded the location and task of each worker at 15-min intervals throughout the 24-h period and noted its interaction with other workers. The result was a time budget for 30 different workers that frequented plant 13 during the 24-h period, from which we could infer how workers of various task specializations used the secondary nest at the plant base.

RESULTS

Secondary Nest Characteristics

Thatch ant secondary nests were found at the base of each plant upon which workers tended Homoptera at Pike Creek during the study period. Viewed from above, secondary nests were simple openings in the ground adjacent to plant trunks (Fig. 1). Ground around an opening was typically littered with thatch material, fallen from the plant canopy, blown in, or excavated from the gallery beneath.

Volume of 10 secondary nests beneath active tending groups of workers ranged from 35 to 125 cc. Secondary nest volume was not significantly correlated with basal plant diameter ($R^2 = .02$, $P > .05$, $N = 10$) but was significantly correlated with number of tenders ($R^2 = .33$, $P < .05$, $Y = .54X + 43.3$, $N = 10$).

Excavations of secondary nests into which labstone had been poured revealed that cavities essentially conformed to morphology of the plant trunk itself (Fig. 2). Thatch ant workers typically removed dirt, small stones, and other debris from within 5–20 mm of the plant trunk, leaving a cavity punctuated with large stones and roots. The nest represented in Figure 2 was 10.8 cm deep and consisted of three separate chambers totaling 175 cc in volume.

Temperature within the secondary nest differed considerably from temperatures recorded simultaneously on the ground surface, in the plant canopy, or deep within the primary nest (Fig. 3). Over the 1-wk period 13–19 June 1987, for example, the secondary nest we measured was an average of about 7°C cooler than 25 cm from the dome top of the primary nest (18.8° vs. 26.1°), with a little over twice the variance over time (12.6 vs. 5.7). Compared to ground surface, the secondary nest was slightly cooler (18.8° vs. 19.2°) but much less variable, exhibiting a variance of about one-ninth the ground surface (12.6 vs. 112.4). Compared to the canopy of the same plant, the secondary nest was slightly warmer on average (18.8° vs. 18.0°) but about one-fifth as variable (12.6 vs. 67.1). Temperature trends over the entire summer were similar to those measured in this 1-wk sample period in mid-June.

Secondary Nest Use

Observations of individually marked workers on plant 13 of colony 2 clearly show that the secondary nest is used throughout the day (Fig. 4). The greatest percentage of workers was found in the secondary nest during mid-afternoon, corresponding to highest daily tem-

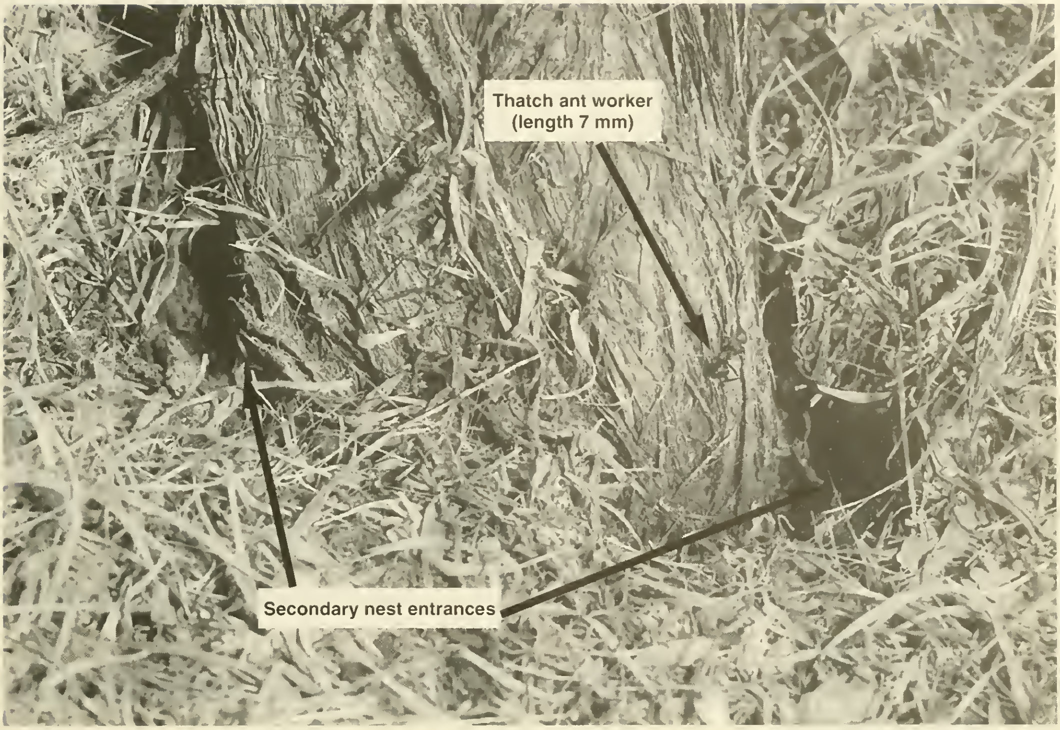


Fig. 1. Aboveground appearance of secondary nest at base of sagebrush plant, Pike Creek, southeastern Oregon, June 1994 (photograph by Trygve Steen).

peratures. Secondary nest population was lowest between 1700 and 2000, and between 0600 and 0900, during principal times when workers deliver honeydew to the primary nest.

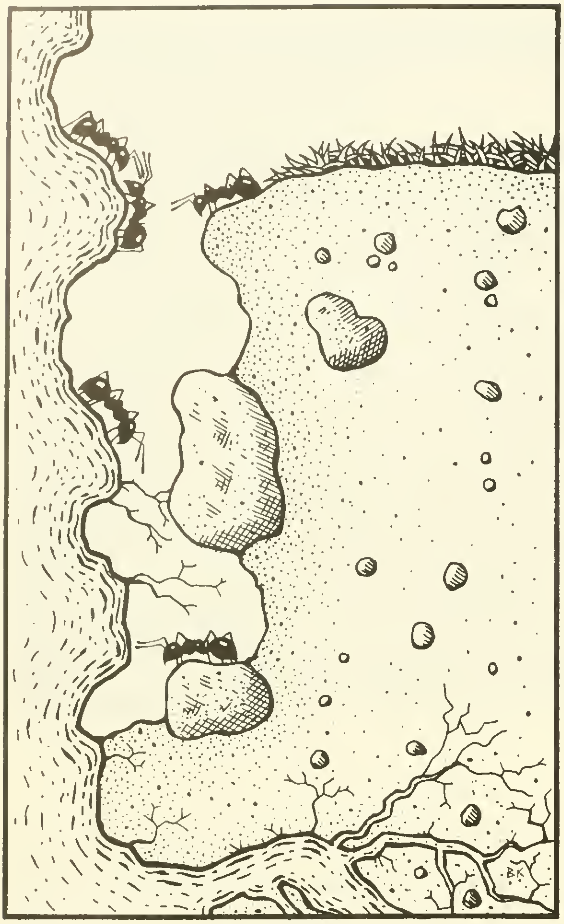
Two typical patterns of activity were observed for plant-associated workers (Fig. 5). **Tenders** spent the majority of their time tending Homoptera for honeydew in the plant canopy. Worker 84, for example, spent 54% of her time tending aphids, with each visit to the plant canopy lasting between 2 min and about 3 h. Her visits to the plant canopy were interspersed with frequent visits to the secondary nest at the plant base, where it is likely she transferred honeydew to larger nontending individuals like worker 13 (chain transport). Twice per day she returned to the primary nest: once in the early evening and once in the morning.

Honeydew **transporters** spend the majority of their time in the secondary nest itself. Worker 13, for example, spent 66% of her time in the secondary nest, 23% scavenging on the ground surface, and 9% on twice-daily returns to the primary nest. On her returns to the primary nest, worker 13 often had a distended gaster, indicating a crop swollen with honeydew. Typically, workers like #13 were scavengers, secondary nest excavators, and/or honeydew transporters, receiving the majority of their honeydew from workers that concentrated on tending Homoptera in the plant canopy.

Of the 30 workers associated with plant 13 during the intensive observation period, 19 were classified as tenders, 6 as honeydew transporters/scavengers, 2 had behavior intermediate between tender and transporter/scavenger, and 3 were not observed often enough to classify.

DISCUSSION

Great Basin Desert thatch ants use secondary nests as a refuge from high midday temperatures and as a site within which honeydew is transferred from workers who collect it in the plant canopy to those who help transport it back to the primary nest. Ground temperatures above 50°C have been reported as lethal to *F. obscuripes* (O'Neill and Kemp 1990), and Mackay and Mackay (1984)



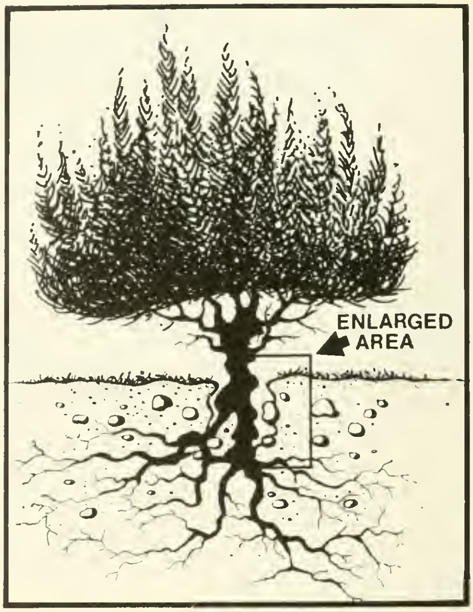


Fig. 2. Scale drawing of secondary nest, taken from photograph of labstone plug, Pike Creek, southeastern Oregon, August 1991.

observed that *F. haemorrhoidalis* workers hide under pine cones or retreat to shady places during midday heat. Chain transport appears to be an effective way to increase delivery of honeydew to the primary nest (McIver and Yandell 1994); thus, it is not surprising that honeydew transfer occurs at a site offering refuge from midday heat.

The use of cool midday refugia by workers may also reduce metabolic costs and increase worker longevity. In a study on fire ant thermal preferences, Porter and Tschinkel (1993) reported that fire ant workers consistently choose cooler temperatures than those selected for the brood. They postulate that this tendency increases longevity of workers not directly associated with brood care. This idea is supported by Calabi and Porter (1989), who demonstrated that because temperature and metabolic rate are highly corrrelated, fire ants reared and maintained under high temperature regimes have lower longevity.

Thatch ants living at other sites in the Great Basin also use secondary nests of this kind (McIver personal observation); Weber (1935) described secondary nests in his study of South Dakota thatch ants. However, Weber reported that the function of these nests was to serve as (1) an arborescent chamber within which to tend Homoptera and (2) a potential site for development into primary nests. Certainly, colonies of *Formica rufa*-group species often reproduce by budding (Mabelis 1979; *F. polyctena*), and the site of a new primary nest is very often a secondary nest (Scherba 1959, McIver personal observation). It is not known whether *F. rufa*-group species living in other habitats employ secondary nests for these or other reasons.

Other *Formica* species are also known to employ secondary nests. The mound-building ant *F. exsectoides* (*exsectoides*-group) uses secondary nests as shelters for treehoppers and as sites for food exchange (Andrews 1929).

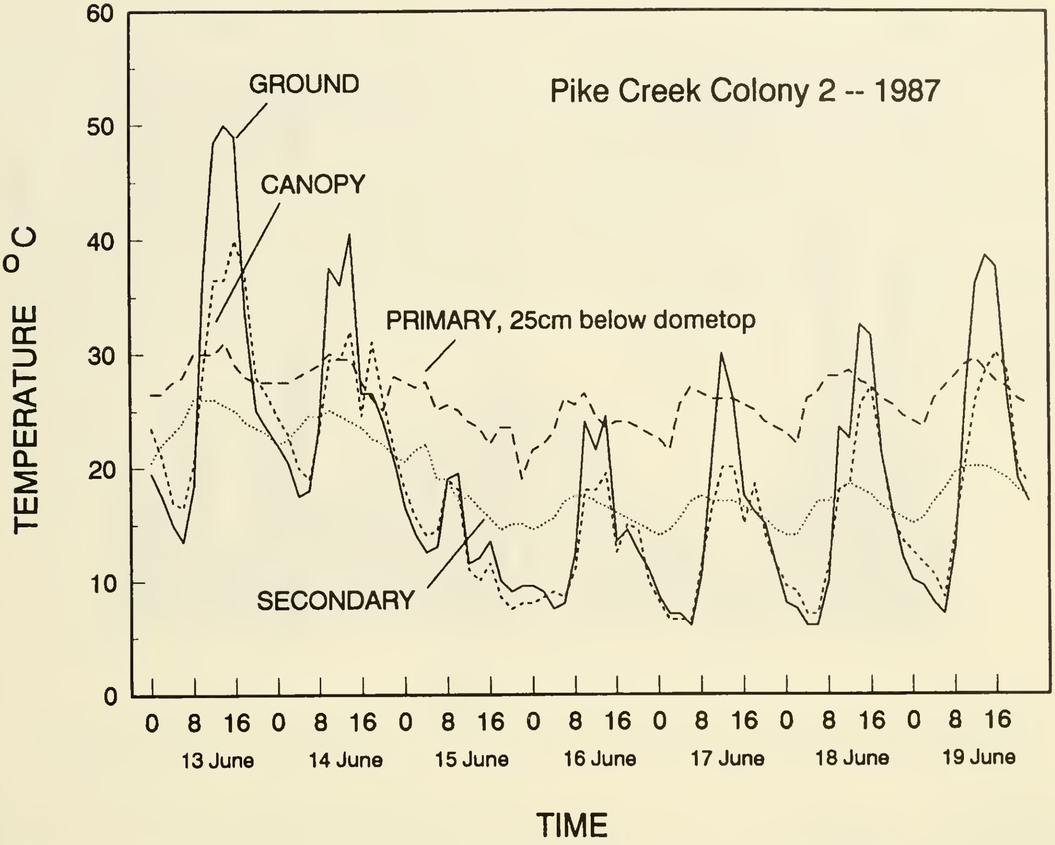


Fig. 3. Temperature (°C) during week of 13–19 June 1987, on ground surface, in sagebrush canopy, 25 cm below dome top of primary nest, and in secondary nest of colony 2, Pike Creek, Oregon.

Formica integra of North America and *F. pratensis* of Europe construct secondary nests along covered paths (Wheeler 1910, Forel 1921).

Other Homoptera-tending ants, including the formicines *Lasius niger* (Forel 1921), *L. emarginatus* (Forel 1921), *L. flavus* (Soulie 1961), and *Polyrachis simplex* (Ofer 1970), and the myrmicines *Crematogaster pilosus* (Forel 1921) and *C. auberti* (Soulie 1961), use secondary nests as shelters for their homopteran symbiotes.

ACKNOWLEDGMENTS

Bryce Kimberling drew the secondary nest from photographs. We thank Courtney Loomis, Deborah Coffey, Joseph Furnish, and Bill Clark for assistance in the field. Jeffrey C. Miller provided the datapod for temperature recordings. Andre Francour kindly identified *Formica obscuripes* Forel. Research was supported by the National Geographic Society and the Systematic Entomology Laboratory of Oregon State University (Dr. John Lattin), where voucher specimens are held.

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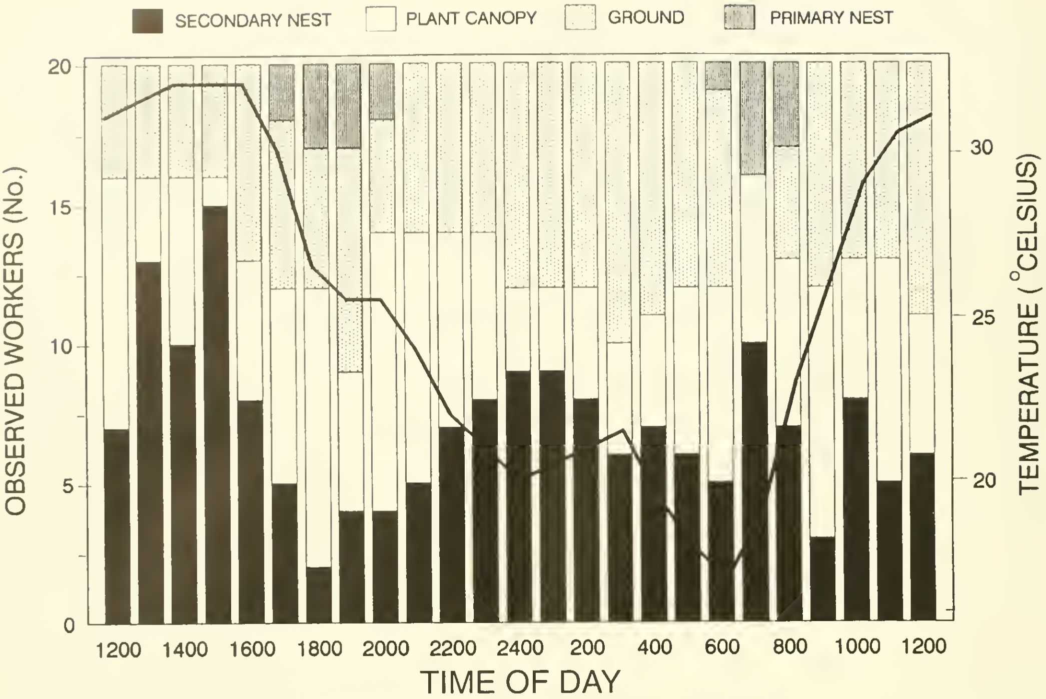

Fig. 4. Activity of marked workers of plant 13, Pike Creek colony 2, 23–24 July 1987. Number of workers observed in secondary nest, in plant canopy, on ground, at primary nest, and temperature in degrees Celsius over 24-h period.

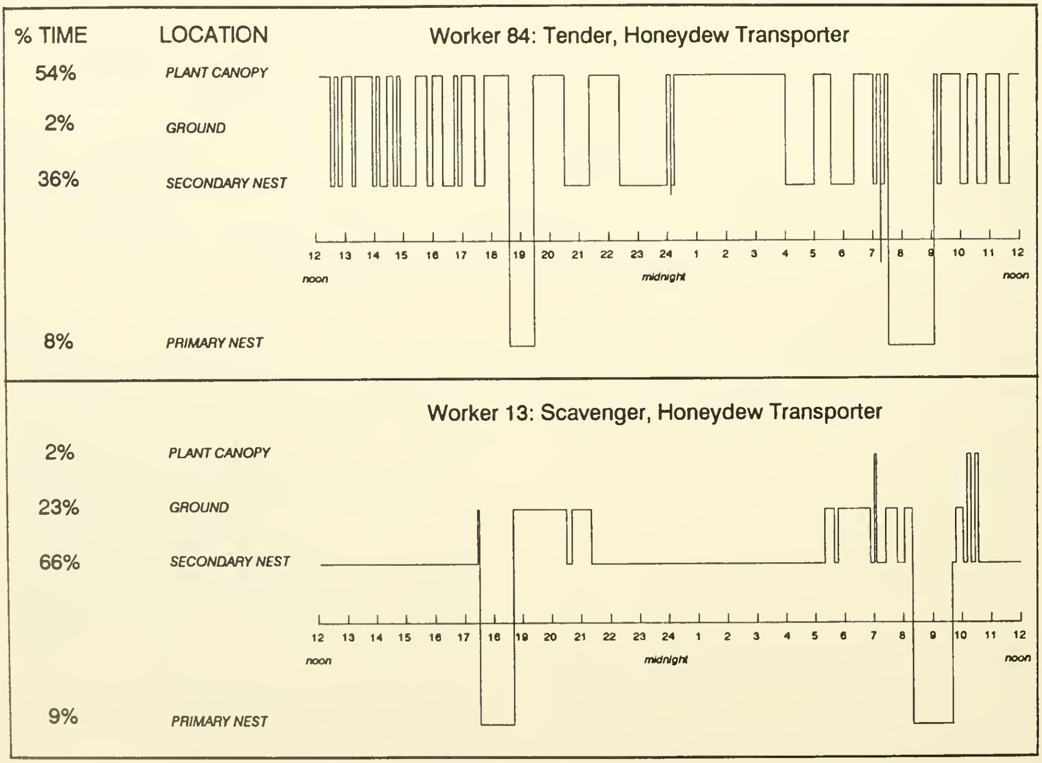

Fig. 5. Activity over 24-h period of workers 84 and 13 on plant 13, colony 2, Pike Creek, Oregon, 23–24 July 1987.

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SPAWNING CHRONOLOGY AND LARVAL EMERGENCE OF JUNE SUCKER (*CHASMISTES LIORUS*)

Timothy Modde [1,2] and Neal Muirhead[1]

ABSTRACT.—June sucker (*Chasmistes liorus*) spawned in the Provo River, Utah, over a 2-wk period in early June during both 1987 and 1988. Emergent larvae emigrated from the river to Utah Lake over a 2- to 3-wk period. Drift into the lake peaked between 1200 and 0400. During daylight hours, emergent larvae tended to occur in pools. Peak emergence of larval drift was approximately 1.2 larvae/m^3 during late June in 1987 and 1988. Recruitment failure of June sucker is not due to reproductive failure.

Key words: June sucker, Chasmistes liorus, *spawning, larvae, habitat, drift, emergence, river.*

The June sucker (*Chasmistes liorus*) is one of three contemporary species of the genus *Chasmistes* (Miller and Smith 1981) and is endemic to Utah Lake, a 38,000-ha remnant of prehistoric Lake Bonneville. Once June sucker numbered in the millions (Jordan 1891) and were one of the most abundant fishes in Utah Lake. During the last century population size of June sucker declined drastically. In a survey of Utah Lake fishes, less than 0.4% of fish collected were June sucker (Radant and Sakaguchi 1981). The population of June sucker has been estimated to be <1000 adults and is listed on the federal register as an endangered species (U.S. Fish and Wildlife Service 1986). Suspected factors contributing to the decline of this species include water loss to irrigation and drought, degradation of water quality, and negative interactions with nonnative fishes (Radant and Hickman 1984). Reduction of water quantity and quality impacted both the lake and spawning tributaries.

The direct cause of decline in the June sucker population has been lack of recruitment (Sigler et al. 1985). In a survey of Utah Lake, Radant and Sakaguchi (1981) did not capture any June sucker <400 mm total length. Scoppettone (1988) reported that June sucker may live to be 42 years of age; thus, in the absence of recruitment, senescent individuals would dominate the population. None of the 18 fish he examined was younger than 20 years of age.

June sucker have been described as spawning on gravel cobble substrate in relatively high-velocity habitats (Radant and Hickman 1984). Sex products are broadcast over the substrate, and eggs are adhesive to the substrate (Shirley 1983, Radant and Hickman 1984). Although information on spawning behavior and larval morphology (Shirley 1983, Snyder and Muth 1988) exists, no information is available on spawning success of the June sucker. Because natality is a vital element of recruitment, information on spawning success is important in understanding declining abundance of this species. The objectives of our study were to (1) estimate timing and magnitude of downstream drift of emergent June sucker larvae and (2) describe habitats occupied by larval June sucker in the Provo River.

METHODS

Drift Sampling

Drift netting was conducted in the lower Provo River to capture emergent larvae during the 1987 and 1988 spawning periods. Netting began 1 June 1987 and terminated when larvae ceased to appear in collections. Five drift nets, each with a mouth size of 30 × 45 cm and a mesh size of 560 microns, were placed at a single site about 3 km upstream of Utah Lake, immediately downstream of the lowermost observed June sucker spawning activity. Nets were anchored with 0.64-cm-diameter rebar along a single transect perpendicular to the channel. When depth permitted, nets were placed alternately at the surface and bottom. In 1988, drift netting using the same sampling scheme began 6 June. The netting site was moved about 50 m downstream of the 1987 site because of physical changes in the channel. Only four nets were used during 1988.

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Nets were set on alternate days (MWF) each week. Each 24-h day was divided into six 4-h periods, and drift was sampled continuously during the middle 1.5 h of each. Starting times were 1315, 1715, 2115, 0115, 0515, and 0915 h. Drift from each net was rinsed, placed in watertight plastic bags, and preserved in 5% buffered formalin; 420 samples were taken.

Velocity (10-sec average) through each net and water depth were measured before and after each set. Volume sampled was estimated by multiplying the average of the two velocity measurements by time sampled and area of the net opening. Water temperature was recorded during each 4-h interval. All samples were sorted for eggs and larvae, which were identified to species (Snyder and Muth 1988), counted, and measured to the nearest 0.1 mm (total length).

Habitat Sampling

Fishes in a 2.25-km section of the lower Provo River were sampled during the 1988 spawning season to determine larval habitat use. Eighty-four transects, about 27 m apart and perpendicular to the thalweg, were established from aerial photographs of the river. Three samples were taken along each transect, one near each shore and one in the middle of the river. Samples were collected with a 1-m^2 bag seine with a 560-micron mesh. Substrate in a 1-m^2 area immediately in front of the seine was mechanically stirred at each sampling site, and the seine was quickly pulled through. Samples were taken only during daylight hours.

Habitat types were described and widths measured along each transect using a modification of Bisson et al. (1982). All fish collected were placed in plastic containers and preserved in 5% buffered formalin. Larvae were identified to species, measured to the nearest 0.1 mm (total length), and counted.

Analysis

Means for egg and larval density in the drift were determined for daily and 4-h periods. Standard deviations were calculated from daily means among periods and for periods with days as replicates. Drift densities were estimated by dividing eggs and larvae collected during each sampling period by water volume passing through drift nets. Daily estimates were determined by computing the means of all six time periods. Estimates of total larvae on the peak drift date were determined by averaging discharge recorded at the Provo City gauge station (USGS) on both days samples were made and multiplying the volume estimate by daily mean larval density.

Because of the few sites in which June sucker larvae were present, habitats were grouped into pool and nonpool categories. Chi-square analysis was used to test the significance of differences in the incidence of larval June sucker in pool and nonpool habitats, and odds ratio analysis (Fienberg 1980) was used to quantify the magnitude of differences observed.

RESULTS

Drift

Spawning, as defined by egg drift, was higher on 3–4 June 1987 and peaked on 6–7 June 1988 (Figs. 1, 2). A malfunction of the velocity meter on 6 and 8 June 1988 prevented accurate estimation of egg and larval concentrations. However, absolute numbers of eggs captured on 7 June (0.007 eggs/sec) and 8 June (0.005 eggs/sec) exceeded those caught on 11 June (0.0007 eggs/sec). Average river temperatures during the spawning period were 13–14°C in 1987 and 12–17°C in 1988. Spawning occurred over a relatively short time; eggs were collected for 1 wk in 1987 and 11 d in 1988. Spawning duration was probably longer in both years than shown in Figures 1 and 2 because eggs were already present in the river when sampling began. However, collections from both years suggested that June sucker spawning activity does not last more than 2 wk, with the greatest number of eggs spawned within a 3- (1987) to 5-d (1988) period.

Density of egg drift was variable and showed no diel pattern (Fig. 3). Thus, either fish were spawning in both light and dark hours or eggs were being randomly dislodged from the

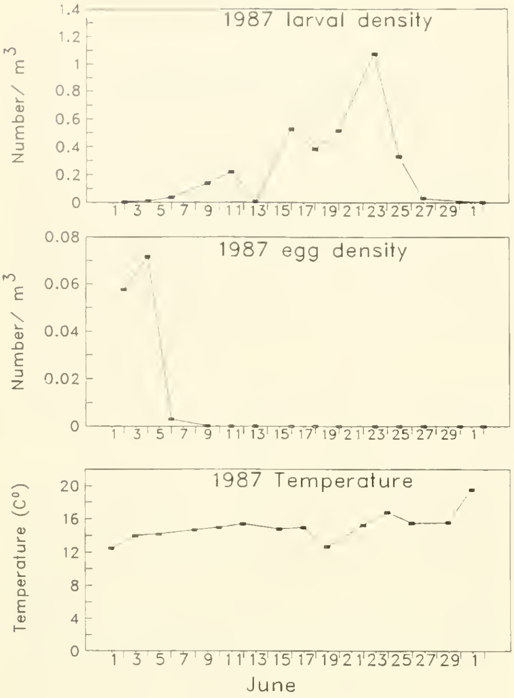

Fig. 1. Drift rates of June sucker larvae and eggs, and daily average temperature collected from the Provo River, Utah, in June 1987.

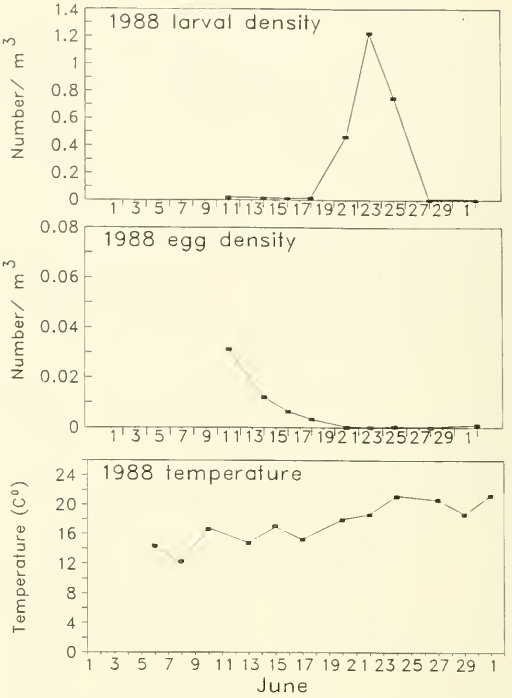

Fig. 2. Drift rates of June sucker larvae and eggs, and daily average temperature collected from the Provo River, Utah, in June 1988.

substrate throughout the 24-h period. During drift netting operations June sucker were observed spawning during both day and night.

Larval June sucker first appeared in the drift on 3 June 1987 and 6 June 1988 (Fig. 1). Although velocity error precluded absolute measurement until after 10 June, few larvae were collected until 20–21 June. Peak densities of larvae in the drift occurred on 22–23 June 1987 and 22–23 June 1988. Minimum estimates of the time between egg deposition and swim-up, measured as the period between peak egg drift and peak larval drift, were 19 d in 1987 and 16 d in 1988. The difference in incubation time between years is probably due to warmer river temperature in 1988 (15–19°C) than in 1987 (12–16°C). Drift of June sucker larvae continued for about 3 wk during both study years. All June sucker larvae collected were identified as either proto- or mesolarvae.

A distinct daily pattern of larval drift density was observed, with most larvae captured between 2000 and 0400 h (Fig. 4). Few larvae were collected in drift nets during daylight. Peak daily estimates of drifting June sucker larvae in the Provo River were approximately 60,200 in 1987 and 73,000 in 1988.

Habitat Use

A total of 57 June sucker larvae were collected in 7 of 115 collections. Incidence of larvae in pool-type habitats was different from nonpool habitats ($X^2 = 7.04$, $.05 = 5.99$). June sucker larvae were 7.5 times more likely to be found in pool than nonpool habitats during daylight hours.

DISCUSSION

Shirley (1983) reported June sucker spawning in mid-June when mean water temperature was between 11 and 13°C. Similar observations were made by Radant and Hickman (1984) and Radant and Sakaguchi (1981). Radant and Hickman (1984) also observed a short spawning period that lasted only 5–8 d. The cui-ui (*Chasmistes cujus*) also spawns during a brief period: males occupying the Truckee River, Nevada, 6.5–16.5 d and females 4.0–10.5 d (Scoppettone et al. 1986). Temperatures of the Truckee River during cui-ui spawning

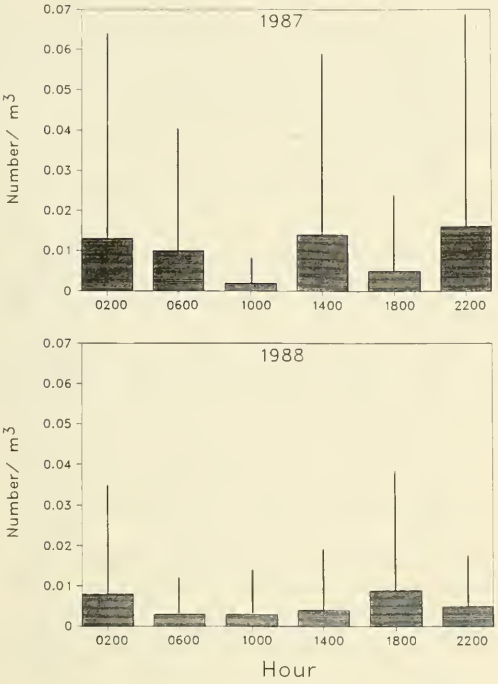

Fig. 3. Diel drift rate of June sucker eggs collected in the Provo River, Utah, in June 1987 and 1988. Vertical bars represent one standard deviation.

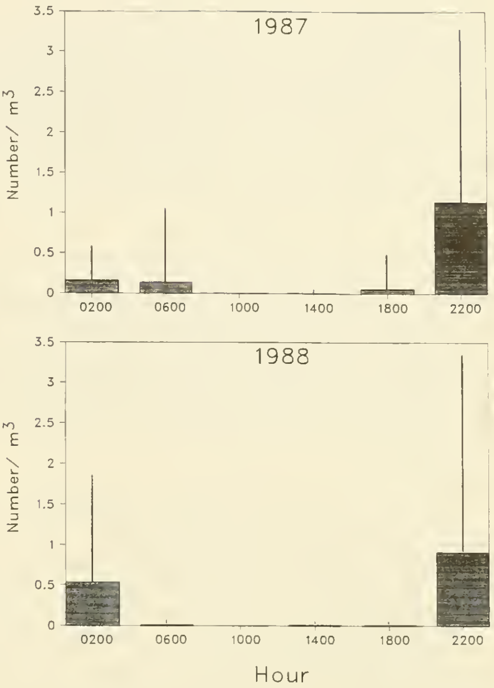

Fig. 4. Diel drift rate of June sucker larvae collected in the Provo River, Utah, in June 1987 and 1988. Vertical bars represent one standard deviation.

ranged from 12 to 15°C. Cui-ui spawned between 2000 and 0600 h during a 3-d period (Scoppettone et al. 1981), whereas egg drift densities of June sucker and observation during both 1987 and 1988 indicated spawning occurred during all hours of the day and night. Scoppettone et al. (1983) reported peak emergence of cui-ui larvae occurred 14 d after peak spawning. Differences between peak June sucker spawning and peak emergence varied between years, from 19 d in 1987 (temperature range 13–15°C) to 16 d in 1988 (temperature range 17–19°C).

Like cui-ui (Scoppettone et al. 1986) and other catostomids (Geen et al. 1966), June sucker larvae emigrate from spawning tributary into receiving lake shortly after emergence. Drift activity of larval June suckers was nearly identical to that of cui-ui, most drift occuring just prior to 0000 and declining to negligible numbers by 0600. In spite of large numbers of larvae captured in the drift, relatively few were captured by seining. Those larvae seined during daylight hours were mostly in pool-type habitats, as reported by both Radant and Hickman (1984) and Shirley (1983). Few, if any, larvae remained in the Provo River for an extended time. Most larvae drifted out of the Provo River during a 2- to 3-wk period, whereas cui-ui were reported to drift through the Truckee River for nearly 30 d. Differences between the two species in duration of larval emergence and drift may result from a larger cui-ui spawning population.

Although the abundant numbers of June sucker larvae produced in 1987 and 1988 are surely less than historic numbers, substantial numbers of larvae drifted into Utah Lake. Sigler et al. (1985) suggested the decline in the Pyramid Lake cui-ui population was due to failure of natural reproduction. Based on the large numbers of larvae captured in the drift, despite the relatively small population of adult June sucker, insufficient spawning or emergent success seemingly did not limit recruitment to Utah Lake. Instead, factors affecting survival after larval emergence, such as nonnative predators, seem likely.

ACKNOWLEDGMENTS

This study was funded by the Utah Division of Wildlife Resources and the U.S. Fish and Wildlife Service. Randy Radant assisted with all phases of the study and provided information on the history of June sucker spawning in the Provo River. Dennis Shirley was instrumental in providing field coordination and logistical support at the study site. Roger Mellinthin, Brad Schmitz, and Don Archer provided field assistance.

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COMPARISON OF REPRODUCTIVE TIMING TO SNOW CONDITIONS IN WILD ONIONS AND WHITE-CROWNED SPARROWS AT HIGH ALTITUDE

Martin L. Morton[1]

ABSTRACT.—Timing of reproduction was assessed for wild onions and White-crowned Sparrows in relation to snow conditions on the same subalpine meadow in the Sierra Nevada for 21 years. Flowering date and clutch initiation date were both highly correlated with snow conditions, being later as snowpack was deeper. Interannual variation in schedule was 46 days for onions and 33 days for sparrows. There was nearly a fivefold difference in snowpack depth, and date of snow disappearance varied interannually by 72 days. Compensation for late-lying snows occurred in both species but was greater in sparrows than in onions because the nest-building behavior of sparrows was flexible. In years of deeper snow, sparrows were able to lay eggs earlier because they built more nests than usual in trees and shrubs rather than waiting for groundcover to develop.

Key words: Allium, Zonotrichia, *snowpack, high altitude, proximate factors, reproduction.*

Montane settings are useful for the study of environmental adaptation in organisms because their brief, sharply delimited growing seasons and variable climates can be potent agents of natural selection. Diurnal and seasonal cycles of abiotic factors, principally air temperature (Ta), moisture, and wind speed, shift in level and amplitude as elevation increases (Rosenberg 1974). The resulting decrease in mean Ta, high winds, decreased availability of soil moisture due to freezing, and variable snowpack can greatly influence the phenology, distribution, and productivity of plants (Billings and Bliss 1959, Scott and Billings 1964, Weaver and Collins 1977, Ostler et al. 1982). Annual schedules of reproduction and survival of hibernating mammals (Morton and Sherman 1978) as well as reproductive success of both sedentary (Clarke and Johnson 1992) and migratory birds (Morton 1978, Smith and Andersen 1985) also are known to be affected, especially by spring storms and snowpack depth. It follows that long-term studies of the annual rhythm of reproduction of organisms at high altitude should provide valuable information for understanding the pathways and scope of adaptations to climatic conditions and for determining the efficacy of environmental variations to act as cues or proximate factors in the control of reproduction schedules. Such studies are few, however, and, to my knowledge, there are none that have compared plants and animals on the same study area. Herein I present 21 seasons of data that index reproductive schedules of the wild onion (*Allium validum*) and the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) at the same location in the Sierra Nevada in relation to interannual variations in snow conditions.

MATERIALS AND METHODS

The study site, Tioga Pass Meadow (TPM), is a subalpine meadow with an area of about 50 ha (0.5 × 1.0 km) and elevation of 3000 m located in the upper end of Lee Vining Canyon, Mono County, California. It is bounded by Tioga Lake on the northern edge and the boundary of Yosemite National Park at Tioga Pass on the southern edge. *Allium validum*, which grows in large clumps in wet meadows at elevations of 1200–3350 m in the Sierra Nevada, is usually 0.5–1.0 m in height and has numerous small (6–10 mm) flowers organized into terminal umbels (Munz 1970). For 21 summers, 1968–70, 1973, 1976, and 1978–93, when I was on TPM daily, I kept notes on the flowering schedule of one particular, fairly compact patch of *A. validum* that covered an area of about 0.1 ha (25 × 40 m) near the center of TPM and that usually contained about 1200 umbels. Technically, flowering includes the period from floral bud initiation through floral persistence (Rathcke and Lacey 1985), but I use the term to describe the date on which buds opened to reveal the mass of flowers within. In any given year this date varied by 2 wk or more among the various patches of *A. validum* scattered across TPM, but flowering within a particular patch, including the study patch, was highly synchronous, occurring within a 3-d period for most individuals. The last day of this opening period was noted every year and is the datum used in this analysis.

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The primary focus of my field studies on TPM was the reproductive biology of *Z. l. oriantha*, a migratory finch that winters in Mexico and breeds in montane meadows of the western United States. Individuals arrive at breeding areas in May and June and depart for wintering grounds in September and October. Wet subalpine meadows like TPM are a preferred breeding ground habitat, but more xeric locations at lower elevations are sometime utilized (Morton and Allan 1990). Nests are built only by females and are placed on the ground or in shrubs, such as willows (*Salix* sp.), or in small trees. Data gathered on banded females included the date they laid their first egg of the season, i.e., the clutch initiation date. Herein I use the mean date of the first 10 clutch initiations on TPM each season to indicate the onset of reproduction in *Z. l. oriantha*. Most nesting data were obtained from females that were frequently observed and trapped (each had a unique combination of color bands), allowing me to follow changes in their behaviors, body weights, and brood patches. This was important to data quality because females quickly renested if a nest was lost from storms or predation.

Information on snow conditions was available because, first, I estimated from direct observations the snowcover on TPM as the season progressed up to the day when all patches of snow had disappeared—the date of 0% snowcover. Second, information on snow depth in TPM could be obtained because it is a site traditionally used by the State of California Department of Water Resources to measure snow depth in order to predict water storage and runoff. Maximum snowpack occurs about 1 April, and this measurement is published in their bulletin 120.

Results

During this study snow depths ranged from a low of 79.0 cm in 1976 to a high of 375.7 cm in 1983. The earliest 0% snowcover date was 1 June 1992, and the latest 11 August 1983, a range of 72 d. The earliest date for onion flowering was 6 July 1968 and 1976, and the latest was 21 August 1983, a range of 46 d. The earliest mean date for clutch initiations, based on the first 10 nests of the season, was 27 May 1992, and the latest mean date was 29 June 1983, a range of 33 d (Table 1). Thus, reproductive schedule in relation to snowpack was affected more in onions than in sparrows. In both species, however, timing of reproduction was highly correlated ($P < .001$) with maximum snowpack (Fig. 1). The final disappearance of snow (0% snowcover) was tightly coupled to snow depth, and flowering and clutch initiation schedules were related accordingly to time of snow disappearance (Table 2). Slope values for the relationship of flowering to both measures of snow conditions (snow depth and 0% snowcover) were about twice those observed for clutch starts in relation to these same two measures (Table 2). Slopes for both comparisons were significantly different (t tests, $P < .001$).

Discussion

Reproduction was delayed by deep, late-lying snow more so in *A. validum* than *Z. l. oriantha*, but there was a compensatory mechanism operating to lessen the temporal impact of heavy snows even in the onion. When flowering date was regressed on snow disappearance date, the slope was 0.53, far less than 1.0 (Table 2). How then does the onion adapt? Only three major physical environmental factors have been identified as cues that initiate flowering: temperature, moisture, and photoperiod (Rathcke and Lacey 1985). Photoperiod-responsive or long-day plants are relatively unaffected by snowpack because they flower and are pollinated late in the summer. In contrast, nonphotoperiod-responsive plants tend to bloom in spring or early summer, and phenophases may be affected by as much as 6 wk by temperature and moisture conditions (Owen 1976). Some plants can "catch up," at least somewhat, by condensing or telescoping phenophases when delayed by overlying snow (Billings and Bliss 1959, Scott and Billings

TABLE 1. Twenty-one years of data on snow conditions, time of flowering in *A. validum*, and mean of clutch initiations and nest locations in *Z. l. oriantha*. The first 10 nests of the season were used to calculate mean date of clutch initiation, and all nests found in a given season were used to calculate percentage of those built aboveground. Number of nests found per season: mean = 59.6, S.D. = 21.9, range = 18-100, total of all years = 1252.

Year	Snow depth (cm)	0% snowcover (Julian day)	Onion flowering (Julian day)	Clutch initiation (mean Julian day)	Aboveground nests (%)
1968	113.5	175	188	160.6	40.0
1969	342.1	215	233	170.1	72.3
1970	176.3	183	198	158.3	34.9
1973	204.2	181	207	163.1	59.3
1976	79.0	158	188	153.8	10.9
1978	263.4	215	222	177.2	50.8
1979	227.1	191	207	160.7	43.6
1980	262.6	214	217	177.0	52.4
1981	173.0	167	197	156.4	25.3
1982	294.4	216	225	169.0	43.8
1983	375.7	224	234	181.3	32.1
1984	205.0	197	208	158.3	44.6
1985	145.8	172	197	156.8	25.5
1986	243.3	213	213	160.9	56.9
1987	113.3	163	201	152.5	18.6
1988	121.2	170	198	161.3	11.1
1989	158.0	176	201	156.2	39.4
1990	90.9	172	196	157.4	30.0
1991	167.4	181	214	164.7	46.7
1992	108.2	152	201	146.8	37.0
1993	227.1	199	216	169.5	49.2

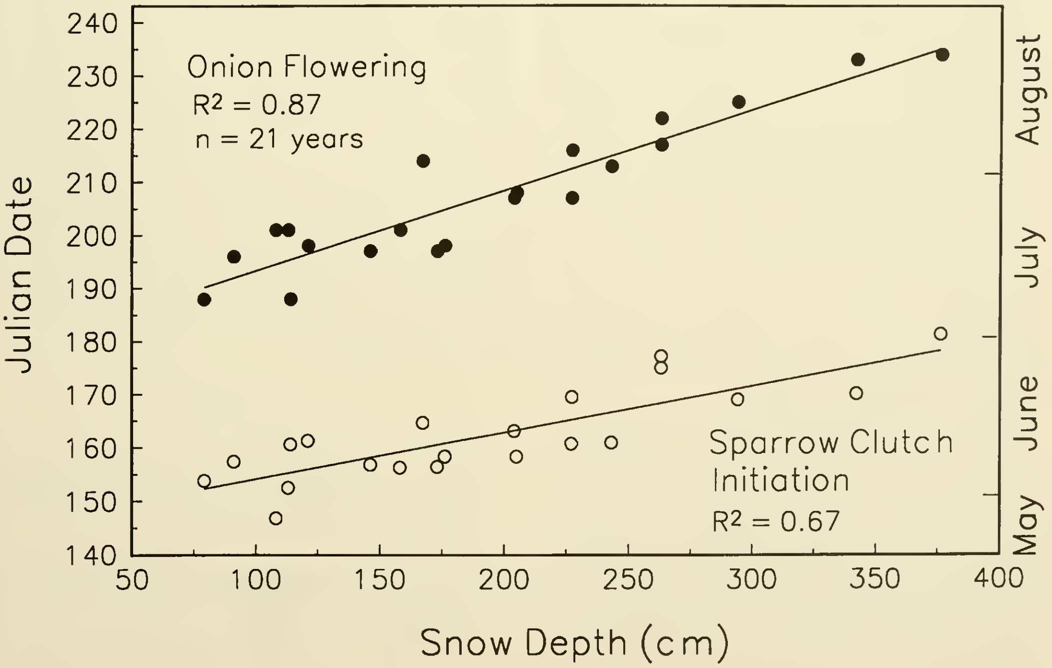

Fig. 1. Date of flowering in *A. validum* and mean clutch initiation in *Z. l. oriantha* as a function of snow depth on 1 April at Tioga Pass Meadow.

TABLE 2. Slopes and coefficients of determination (R^2) for linear regressions involving date of flowering in *A. validum* and mean date of clutch initiation and percentage of nests placed in sites off the ground in *Z. l. oriantha* in relation to snow conditions (snow depth on 1 April and date of 0% snowcover) at Tioga Pass Meadow. $N = 21$ years.

Y	X	Slope	R^2 (%)	P
0% snowcover	Snow depth	0.25	86.1	<.001
Flowering date	Snow depth	0.15	86.9	<.001
Flowering date	0% snowcover	0.53	76.1	<.001
Clutch initiation date	Snow depth	0.09	68.9	<.001
Clutch initiation date	0% snowcover	0.34	75.7	<.001
Aboveground nests	Snow depth	0.12	40.2	.002
Aboveground nests	0% snowcover	0.47	42.4	.001

1964, Weaver 1974, Weaver and Collins 1977). Alpine plants often store large quantities of carbohydrate in underground organs; mobilization of these reserves to shoots can occur even before snowcover is gone. Relatively high carbohydrate levels are then maintained in the shoot portion until after fruiting, whereupon a return of peak reserve levels to underground parts occurs at the beginning of fall dormancy (Mooney and Billings 1960). The mechanism whereby events in the growing season can be accelerated has not been studied to my knowledge, but this seasonal cycle of transport and utilization of stored energy must be a vital constituent.

A puzzling aspect of *A. validum*'s flowering response is that it was strongly affected by snow conditions, typical of nonphotoperiod-responsive plants that usually flower in May or June. *A. validum* flowers in July or August, a time that is more typical of plants cued by long days (Owen 1976). Perhaps *A. validum* has seasonal changes in its photoresponsivity and is following a mixed strategy energetically, using stored reserves early in the season and then later switching to a greater reliance on photosynthate of the current year, the latter being a trait common to photoperiodic species (Mooney and Billings 1960).

The lessened impact of snow conditions on reproductive schedule in *Z. l. oriantha*, as compared to *A. validum*, appears to occur because the bird has flexible nest-building habits. Only about 11% of all nests constructed at TPM in dry years, such as 1976, were placed in aboveground sites (Table 1). In wet years, such as 1969, when snowpack was unusually heavy, this increased to 72% (Table 1). The 1983 data seem anomalous, but hot spring weather induced rapid snowmelting, and more nests were placed on the ground than might have been otherwise expected. The main point here is that when groundcover was adequate for hiding nests, females seemed to prefer nesting on the ground. When plant growth and development were impeded by late-lying snow, they did not wait a long period for this cover to develop, but instead built a greater proportion of their nests aboveground, usually in pines (*Pinus* sp.) and willows. Thus, behavioral plasticity in selection of nesting sites allowed *Z. l. oriantha* to proceed with rearing young with less delay than might be predicted from snow conditions or even from plant phenophases.

In summary, this correlative study presents temporal indices of reproductive schedules during 21 years in a plant and an animal occupying the same high-altitude environment, thus permitting a comparison of their responses to a proximate or environmental factor experienced in common, namely interannual variation in snowpack. Both organisms were affected by this factor and both exhibited compensatory adjustments of their schedules. The adjustment was greater in the animal because it possesses a basic trait, not present in the plant, that can be acted on by natural selection, its behavior.

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OPPORTUNISTIC BREEDING AFTER SUMMER RAINS BY ARIZONA TIGER SALAMANDERS

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Key words: Ambystoma, *Arizona, amphibians, opportunistic breeding.*

Identifying factors influencing the number of times organisms breed during a lifetime and the seasonal timing of reproductive episodes is central to understanding the evolution of life history traits (Stearns 1992). In this regard, amphibian reproductive cycles are often considered adaptations to the seasonality of oviposition opportunities (Joly 1971, Lofts 1974, Salthe and Mecham 1974). This is seen in most north temperate zone amphibians that breed in temporary aquatic habitats and have annual reproductive cycles (Bishop 1947, Wright and Wright 1949). These frogs and salamanders typically come into reproductive condition once a year at the same time of year, often in spring as ephemeral habitats predictably fill from snowmelt or winter rains. Where aquatic habitats fill unpredictably or irregularly, such as in dry temperate or tropical regions, amphibians may have acyclical reproductive periods allowing them to breed opportunistically (Salthe and Mecham 1974, van Beurden 1979). Opportunistic breeding in ephemeral habitats is commonly understood as an adaptation for avoiding predaceous fish (e.g., Webb 1969, Heyer et al. 1975, Wilbur 1977, Collins and Wilbur 1979).

Tiger salamanders (*Ambystoma tigrinum* Green) range across North America and have an obligatory aquatic larval stage (Stebbins 1985). Like most ambystomatids (Bishop 1947), the six subspecies of tiger salamanders in western USA (*californiense, mavortium, nebulosum, diaboli, melanostictum, stebbinsi* [Collins et al. 1980, Jones et al. 1988]) all breed in late winter, spring, or even early summer at high elevations. Differences between populations in the timing of the primary breeding period correspond to differences in availability of water in their breeding habitats (Houghton 1976). Some *A. t. mavortium* populations breed both in spring and in summer (Webb and Roueche 1971), and Tanner et al. (1971) documented *A. t. nebulosum* breeding in spring and summer in a continuously filled lake. In this study we report that *A. t. nebulosum* populations can also breed twice per year in ponds that fill with water during the winter, dry during the late spring and early summer, and refill during summer rains.

Arizona tiger salamanders (*A. t. nebulosum*) are found commonly at high elevations in montane Colorado and Utah (Stebbins 1985) and in Arizona between 1500 and 2900 m (Collins 1981). Aquatic habitats discussed in this study are in Rocky Mountain montane conifer forest (Pase and Brown 1982).

Arizona tiger salamanders breed regularly in late winter and spring following snowmelt (Sexton and Bizer 1978, Collins and Cheek 1983, Holomuzki 1986, Jones and Collins 1992). During the course of other fieldwork, we realized that a second breeding pattern also occurs. Here, we present observations that led us to conclude that these tiger salamanders can breed "opportunistically," defined as any breeding outside the usual late winter and early spring breeding period.

On 30 March 1990 we noted typical spring oviposition activity when we observed thousands of *A. t. nebulosum* eggs in Horseshoe Lake (34°22′53″N, 111°14′38″W) on the Mogollon Rim in central Arizona. We visited the lake again on 6 August 1990, before summer rains began. It was completely dry at this time, and we photographed thousands of desiccated salamander larvae on the lake bed. We presumed this represented elimination of the spring 1990 cohort. We sampled this lake again on 23 September 1990 after it had refilled following summer rains and noted several hundred small *A. t. nebulosum* larvae. Live measurements were taken from a sample of larvae on 29 September and compared to measurements taken from projections of two close-up slides of some of the dead spring cohort. We also visited other ponds in this region that had dried and refilled to gauge the extent and success of this breeding tactic.

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Larvae caught in Horseshoe Lake in September were either a second cohort that hatched after summer rains, or animals from the spring cohort that survived the lake drying, presumably by burrowing. Metamorphosed tiger salamanders burrow in soft lake mud (Webb 1969), but this has not been reported for larvae or branchiate adults.

Dead larvae photographed in August averaged 51.4 mm total length (SE = 1.20 mm, N = 35), and larvae collected in September averaged 35.8 mm total length (SE = 0.78 mm, N = 96). If animals collected in September survived drying by burrowing, they should have been at least as large as the dead animals observed in August. Animals in September were, however, significantly smaller than those photographed in August (t = 10.53, P <.0001). This is a conservative test since animals photographed in August were dried and therefore smaller than at death.

We do not consider summer breeding to be the primary breeding event for this population. Because we observed several thousand eggs in March, we conclude that there was a normal spring breeding. Typical larval densities (estimated by drop-box and seining through a measured volume of water) in this part of Arizona in June are 2–75 salamanders m^{-3} (Pfennig et al. 1991). The low density of larvae we estimated in September, 0.3 salamanders m^{-3}, supports the conclusion that there was a second reproductive episode in which a small number of animals bred opportunistically in Horseshoe Lake during 1990.

Adult salamanders breeding in Horseshoe Lake in late summer 1990 were taking advantage of a newly filled habitat. At least some larvae in this second 1990 cohort overwintered successfully (M. Loeb personal observation, 4 May 1991). In 1990, Charco Tank (34°07′50″N, 110°07′32″W) in the White Mountains dried following drought conditions that also dried Horseshoe Lake. In spring 1991 we collected larvae several centimeters larger than recently hatched salamanders in this tank, suggesting salamanders produced a second cohort in this tank following rains in summer 1990. Cottonwood Tank (34°08′43″N, 110°09′06″W) dried in June 1992. Although we did not visit this habitat later in 1992, presence of a large larva in March 1993 (before the spring cohort hatched) suggests opportunistic breeding in summer 1992.

Late-season breeding may, however, fail. Johnnie Tank (34°10′06″N, 110°04′02″W) in the White Mountains is at the same elevation as 13 ponds in the surrounding 180 km^2. Breeding at all other ponds in this area was completed by late March in 1992 and 1993. Johnnie Tank dried in early spring 1992 and then refilled in late May after early monsoon rains. Hatchlings produced by opportunistic breeding following this refilling were all killed when the tank dried again in late June. Because the May oviposition does not overlap the usual breeding season in this area, we consider this to be opportunistic breeding.

Other evidence suggests that summer breeding is exhibited regularly in this subspecies. Metamorphosed females with yolked follicles were recorded in Arizona by Durham (1956) on 18 July on the Kaibab Plateau and by J. Collins (unpublished observation) on 11 July 1980 in the White Mountains.

Tanner et al. (1971) reported sizes of *A. t. nebulosum* larvae in Salamander Lake, a permanent lake in Utah. While following growth of larvae throughout July and August, they recorded a small size class beginning in late July, which they interpreted as evidence of a second breeding. A pattern of spring and fall breeding in permanent ponds with unpredictability in seasonal rainfall is also reported for *Triturus alpestris apuanus* in Italy (Andreone and Dore 1992). Despite the fact that we regularly visit a few dozen continuously filled ponds in Arizona, we have never observed a second breeding in one. Our observations, consistent with the hypothesis outlined below, emphasize that the natural history we are describing for *A. t. nebulosum* in Arizona differs importantly from that reported in Utah.

Webb (1969) argued that an irregular breeding pattern is among the traits that adapt *A. t. mavortium* for life in the Chihuahuan Desert in southern New Mexico; i.e., this subspecies reproduces whenever water fills the ephemeral ponds in which it commonly breeds. *A. t. mavortium* breeds every year in ponds that fill in winter or spring, but may also breed after summer rains. Our data suggest *A. t. nebulosum* in Arizona has evolved a similar life history tactic. In general, breeding occurs following snowmelt at high elevations, but there are some conditions under which individuals will breed opportunistically following summer rains.

An amphibian larva from a spring cohort is not guaranteed sufficient time to complete development to metamorphosis in any aquatic habitat that can dry unpredictably. This is an explanation for iteroparity in most ambystomatids using temporary or "most nearly permanent" ponds (Wilbur 1977). It might be adaptive, however, for adults to take advantage of ponds whenever they refill. In contrast, late-season breeding in permanent aquatic habitats is generally not advantageous since these habitats may harbor older larvae or fish that can prey on embryos and hatchlings (Burger 1950, Reese 1968, Webb and Roueche 1971; but see Dodson and Dodson 1971 and Collins and Holomuzki 1984). Breeding after a habitat refills would be advantageous as the drying would eliminate fish or older larvae. A second advantage of breeding opportunistically arises since metamorphosis is only possible after a minimum size is achieved (Wilbur and Collins 1973), and in temporary ponds like those we report here, this size may not be attained before the pond dries; however, larvae from summer cohorts that successfully overwinter will have a growth advantage over larvae from spring clutches.

A closer examination of the life histories of other subspecies of tiger salamanders found in the arid and semiarid western USA might reveal that regular breeding in late winter and spring, with opportunistic breeding in summer, also occurs in these subspecies.

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VEGETATION RECOVERY FOLLOWING FIRE IN AN OAKBRUSH VEGETATION MOSAIC

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Key words: fire, oak, secondary succession, soil erosion, shrub, grass, ecosystem.

Fire plays a role in maintaining ecosystem diversity, improving forage production, enhancing wildlife habitat, and recycling nutrients in the soil (Wright and Bailey 1982). Postfire succession in the Gambel oak (*Quercus gambelii*) type, however, has received less attention in the literature than most major vegetation types. The most extensive work on secondary succession in the Gambel oak type was done by McKell (1950).

In August of 1990 an intense wildfire burned nearly 3000 ac of oak-dominated vegetation in the vicinity of Wasatch Mountain State Park near Midway, Utah. This note reports on the first-year vegetation recovery in a vegetation mosaic of oakbrush and sagebrush-grass communities during the first year following that fire.

Individual study sites are located in Heber Valley near the town of Midway, Utah. All are in the lower foothill zone of the central Wasatch Mountains. Gambel oak dominates the hillside vegetation of Heber Valley and grows in a discontinuous belt extending from approximately 1500 to 2600 m elevation. Study sites lie within the ecotone near the lower margin of the scrub-oak belt and the upper margin of the foothill zone. The ecotone comprises a vegetation mosaic of open spaces and oak-clone thickets. Major shrub or tree species associated with Gambel oak include *Prunus virginiana, Acer grandidentatum, Symphoricarpos oreophilus,* and *Amelanchier alnifolia.*

Interspersed among oak-clone thickets are open spaces containing vegetation characteristic of both the mountain shrub community and the foothill zone. The interspaces characteristically support populations of *Artemisia tridentata, Purshia tridentata, Chrysothamnus viscidiflorus, Bromus tectorum,* and *Agropyron spicatum.*

Climate of the Heber Valley area is characteristically continental. Annual precipitation at the Heber City weather station averages 39 cm. Mean annual snowfall is 175 cm. Annual average daily maximum and minimum temperatures are 16.1°C and –2.6°C, respectively. The frost-free period is typically 70–80 days (USDA 1976).

One study site was selected within the burn, and a similar nearby unburned area was chosen to provide comparison. Sites were selected for similarity of elevation, aspect, slope, and soils. The burned site (T3S R4E S33 SE1/4) within an elevation range of 1771–1832 m consists of two opposing slopes, one with a generally east-facing aspect, the other generally west-facing. Variability in topography allowed for sampling across a full range (0–360°) of aspect.

The unburned site consists of a roughly circular sampling transect centered on Memorial Hill (T3S R4E S35 NE1/4). The sampling elevation ranges from 1740 to 1771 m. Slopes of both sites range from 20 to 60%. Soils consist of a complex of Hennefer silt loam and Hennefer cobbly silt loam (Pachic argixerolls; USDA 1976). Runoff is rapid on Hennefer soils and erosion hazard is considered high.

Burned and unburned sites were identified for intensive sampling and quadrat analysis. Two supplemental sites of similar slope, elevation, and topography were selected for reconnaissance survey and identified as area C (T3S R4E S21 NE1/4) and area D (T3S R4E S23 NE1/4). Comprehensive species checklists were compiled for all sites to establish whether

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the intensive study sites were representative of vegetation of the vicinity as a whole (Poreda 1992).

Sampling was done in mid-June, early August, and late September during the 1991 growing season. For the reconnaissance surveys, species were recorded as encountered while the surveyor walked arbitrarily selected transects within each of the four study areas. This permitted observation of additional species not found in the quadrats.

Quadrat sampling was conducted along transect lines established on both the burned and unburned sites. Quadrats (1.0 m^2) were marked at 30-m intervals along each transect line. The burned site contained 171 quadrats, the unburned site 39.

Cover for each species, total vegetative cover, bare soil, rock, and litter were estimated within each quadrat using a procedure slightly modified from Daubenmire (1959). The modification consisted of adding one extra cover class with limits of 0–1%. This modification provided a more accurate estimate of cover for small or subordinate species (Davis and Harper 1989). Plant densities were based on counts of individuals (by species) rooted within the 1.0-m^2 quadrats. Species frequencies were the percentage of quadrats in which a species occurred.

Values for cover-class and density were recorded for each species for each quadrat along with sampling date and community type. Species mean percent cover (%C) was computed separately for oak and shrub-grass communities (including aggregated communities) on both the burned and unburned sites. The Mann-Whitney test was used for significance testing of mean differences. Percent of total cover (%TC) of each species was expressed as a percentage of the summed maximum cover of all species. Species identification follows Arnow et al. (1980).

Total vegetative cover was substantially reduced for both communities on the burn even after one full year compared to that of the unburned site (Table 1). Changes in bare soil June through September on both unburned sites are not statistically significant ($P > .28$), nor is the change between June and September on burned shrub-grass sites ($P > .4$). On burned oak sites, however, the trend of significantly ($P = .0004$) decreasing bare soil can be attributed to the dramatic increase in vegetative cover.

Species count (Table 2) on burned shrub-grass quadrats (73) was 1.87 times the number on unburned quadrats (39). Total number of species on burned oak sites (61) was 1.33 times greater than the number on unburned sites (46). The data strongly indicate that shrub-grass sites are richer in species than oak sites, and that this relationship holds even after fire. Moreover, species diversity is higher on both communities following fire.

Many species declined in both frequency and cover following fire (Tables 3, 4). Others increased in both frequency and cover following fire. A few showed little change.

On shrub-grass sites species showing greatest decrease include *Agoseris glauca*, *Agropyron spicatum*, *Artemisia tridentata*, *Crepis acuminata*, *Lathyrus pauciflorus*, and *Lomatium triternatum*. Species increasing after

TABLE 1. Seasonal areal coverage (%C)[a] of vegetation, litter, bare soil, and exposed rock for burned and unburned sites[b].

	Shrub-grass			Oak		
	June	Aug	Sept	June	Aug	Sept
BURNED						
Vegetation	16.79	12.87	28.14	16.30	41.59	49.50
Litter	6.76	21.67	22.86	7.22	9.21	11.57
Bare soil	35.72	37.38	37.98	42.88	33.63	32.44
Rock	18.09	18.74	19.41	10.28	10.25	10.15
UNBURNED						
Vegetation	46.09	31.59	49.50	73.94	65.06	73.18
Litter	37.30	53.95	60.27	88.52	90.59	92.65
Bare soil	7.95	9.05	8.93	6.53	0.79	0.65
Rock	18.80	18.80	19.34	3.09	3.09	2.94

[a] %C expressed as mean cover based on m^2 quadrats.
[b] $n = 171$ (burned); $n = 39$ (unburned).

TABLE 2. Cumulative number of species[a] observed in sampled quadrats.

	Shrub-grass		Oak		Aggregated	
	#	%	#	%	#	%
BURNED						
Total	73	100	61	100	80	100
Annual	24	33	20	33	26	32
Forb	33	45	28	46	36	45
Grass	9	12	4	6	9	11
Shrub	7	10	9	15	9	11
UNBURNED						
Total	39	100	29	100	46	100
Annual	10	26	9	31	14	30
Forb	16	41	9	31	17	37
Grass	8	20	6	21	8	17
Shrub	5	13	5	17	7	15

[a] June through September 1991

TABLE 3. Frequency and cover for major species on shrub-grass sites.

	Unburned			Burned		
Species	Freq.	%C	%TC	Freq.	%C	%TC
Agoseris glauca	9.10	.05	.07	.00	.00	.00
Agropyron spicatum	63.60	10.31	16.04	9.80	.80	2.11
Amelanchier alnifolia	.00	.00	.00	1.60	.05	.13
Artemisia tridentata	27.30	4.59	7.15	.00	.00	.00
Aster chilensis	9.10	.16	.25	3.30	.50	1.30
Bromus tectorum	68.20	6.84	10.64	70.50	6.51	17.14
Chenopodium album	.00	.00	.00	24.60	1.41	3.72
C. leptophyllum	.00	.00	.00	19.70	.50	1.32
Collinsia parviflora	18.20	.21	.32	26.20	.34	.88
Crepis acuminatum	54.50	2.16	3.36	4.90	.07	.17
Galium uparine	4.50	.02	.04	24.60	.52	1.38
Lathyrus pauciflorus	13.60	.84	1.31	3.30	.05	.13
Lomatium triternatum	27.30	.91	1.41	4.90	.02	.06
Machaeranthera canescens	.00	.00	.00	9.80	.40	1.06
Poa pratensis	27.30	6.14	9.56	18.00	2.39	6.28
Polygonum ramosissimum	4.50	.02	.04	19.70	.26	.69
Prunus virginiana	.00	.00	.00	3.30	.30	.78
Quercus gambelii	22.70	5.49	8.55	14.80	1.59	4.17
Solidago sparsiflora	.00	.00	.00	4.90	.54	1.42
Symphoricarpos oreophilus	.00	.00	.00	4.90	.11	.28
Verbascum thapsus	.00	.00	.00	19.70	.90	2.37
Viguiera multiflora	.00	.00	.00	36.10	2.53	6.67

burning include *Chenopodium album, C. leptophyllum, Collinsia parviflora, Galium aparine, Machaeranthera canescens, Polygonum ramosissimum, Solidago sparsiflora, Verbascum thapsus*, and *Viguiera multiflora.*

Some species, such as *Aster chilensis*, may be somewhat less typical in that frequency was lower on burned shrub-grass sites, yet cover was actually greater than on unburned sites (Table 4), suggesting a response of increased size and vigor of the surviving individuals.

Relative to the unburned, *Bromus tectorum* showed little difference in frequency or cover, suggesting only a minor effect in the first year following fire; relative importance of this species was, however, enhanced due to the decline of most other species. Studies by Young and Evans (1978) suggest a potential explosive increase of *B. tectorum* in the second and third years after fire as the species rapidly colonizes space made available by fire.

On oak-dominated sites there was a similar or greater reduction of those same species exhibiting a lowered frequency on shrub-grass sites. In addition, *Aster chilensis* and *Bromus tectorum* (species showing substantial survival

TABLE 4. Frequency and cover for major species on oak-dominated sites.

Species	Unburned			Burned		
	Freq.	%C	%TC	Freq.	%C	%TC
Agoseris glauca	11.80	1.06	1.10	.90	<.01	.01
Agropyron spicatum	29.40	.59	.61	.00	.00	.00
Amelanchier alnifolia	23.50	1.09	1.13	8.10	.95	1.66
Artemisia tridentata	17.60	1.09	1.13	.00	.00	.00
Aster chilensis	5.90	.03	.03	.00	.00	.00
Bromus tectorum	23.50	4.17	4.33	18.90	.16	.28
Chenopodium album	.00	.00	.00	24.30	1.24	2.15
C. leptophyllum	5.90	.03	.03	19.80	.39	.67
Collinsia parviflora	29.40	.15	.15	27.90	.32	.56
Crepis acuminata	47.10	1.38	1.44	3.60	.02	.03
Galium aparine	11.80	.21	.21	24.30	.69	1.20
Lathyrus pauciflorus	58.80	2.59	2.68	7.20	.30	.52
Lomatium triternatum	35.30	.77	.79	1.80	.01	.02
Machaeranthera canescens	.00	.00	.00	.90	.03	.05
Poa pratensis	52.90	16.81	17.44	17.10	1.23	2.14
Polygonum ramosissimum	.00	.00	.00	6.30	.03	.05
Prunus virginiana	29.40	8.38	8.69	10.80	.84	1.46
Quercus gambelii	100.00	51.12	53.03	92.80	38.36	66.68
Solidago sparsiflora	.00	.00	.00	2.70	.19	.33
Verbascum thapsus	.00	.00	.00	19.80	1.12	1.95
Viguiera multiflora	.00	.00	.00	24.30	.86	1.49

on shrub-grass sites) were virtually eliminated from oak-dominated sites. Higher burn temperatures associated with oak-dominated vegetation were likely more damaging to these species. Shrubs most common to oak sites, *Prunus virginiana* and *Amelanchier alnifolia*, both had decreased frequencies following fire. *Amelanchier alnifolia*, however, exhibited more vigorous resprouting. Although frequency was lower on burned oak sites, cover of *A. alnifolia* one year after the burn was only slightly less on the burn site than on the unburned sites.

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